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A Journal of Entomology

Volume 74

1967

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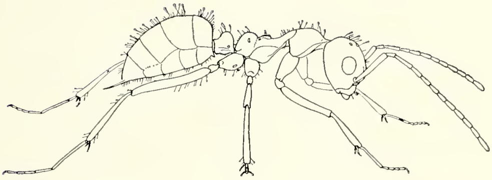

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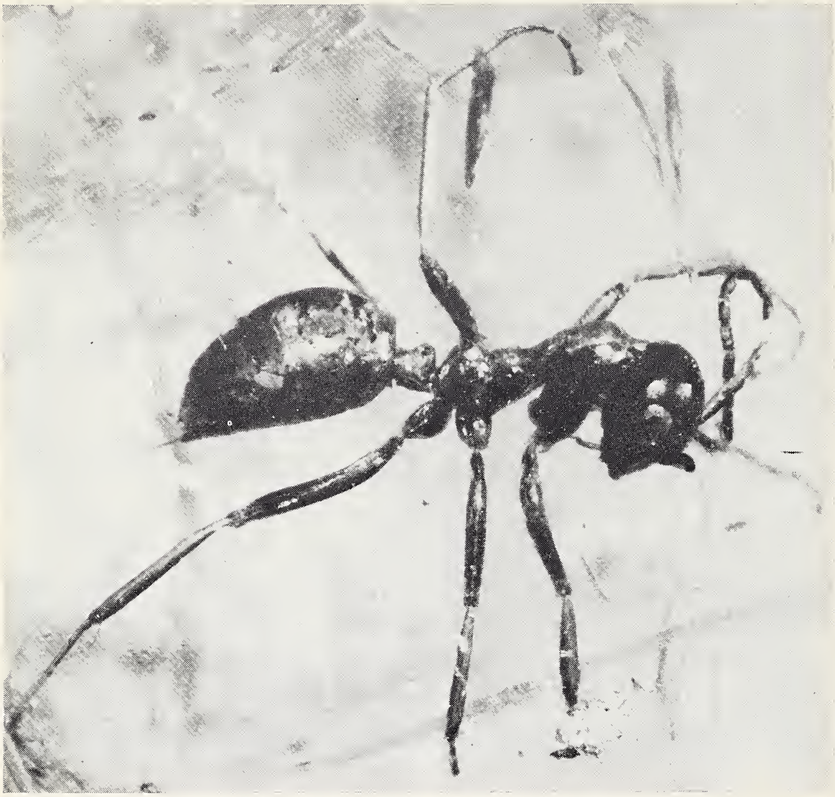

Sphecomyrma freyi, worker no. 1, holotype.

PSYCHE

Vol. 74 March, 1967 No. 1

THE FIRST MESOZOIC ANTS, WITH THE DESCRIPTION OF A NEW SUBFAMILY

By

Edward O. Wilson,[1] Frank M. Carpenter,[1]
and William L. Brown, Jr.[2]

Introduction

Our knowledge of the fossil record of the ants, and with it the fossil record of the social insects generally, has previously extended back only to the Eocene Epoch (Carpenter, 1929, 1930). In the Baltic amber and Florissant shales of Oligocene age, and in the Sicilian amber of Miocene age, there exists a diverse array of ant tribes and genera, many of which still survive today (Emery, 1891; Wheeler, 1914; Carpenter, 1930). The diversity of this early Cenozoic ant fauna has long prompted entomologists to look to the Cretaceous for fossils that might link the ants to the non-social aculeate wasps and thereby provide a concrete clue concerning the time and circumstances of the origin of social life in ants; but until now no fossils of ants or any other social insects of Cretaceous age have come to light (Bequaert and Carpenter, 1941; Emerson, 1965) and we have not even had any solid evidence for the existence of Hymenoptera Aculeata before the Tertiary.

There does exist one Upper Cretaceous fossil of possible significance to aculeate and thus to ant evolution. This is the hymenopterous forewing from Siberia described by Sharov (1957) as *Cretavus sibiricus*, and placed by him in a new family Cretavidae under the suborder Aculeata. As Sharov notes, the wing venation of *Cretavus* does resemble that of the bethyloid (or scolioid) wasp family Plumariidae, a group that has been mentioned in connection with formicid origins. The *Cretavus* wing is also similar to that of such primitive Tiphiidae as *Anthobosca* (see figures, discussion and references in Brown and Nutting, 1950). But the difficulty with this fossil is that we have only the wing, and there is no guarantee that

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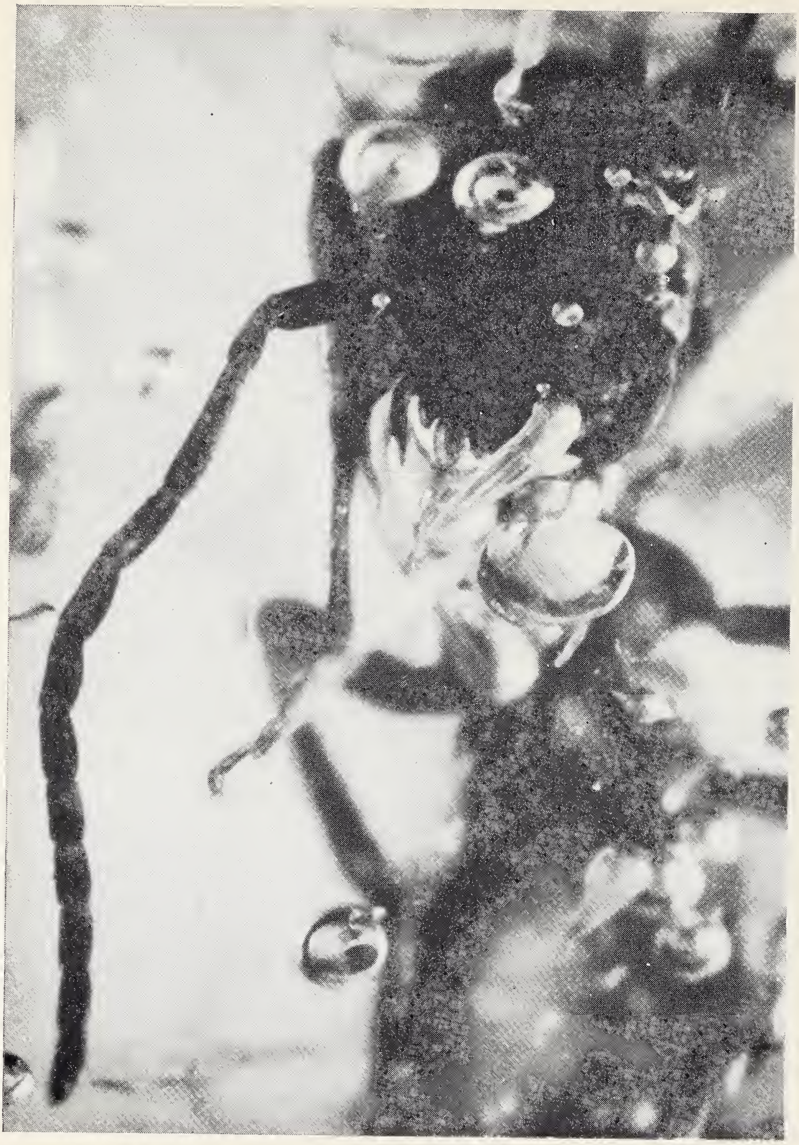


Wilson, Carpenter, Brown — Mesozoic Ants the evolution of venational and body traits proceeded concordantly before, during or after the transition from parasitic to aculeate Hymenoptera. In other words, we do not know from the present evidence whether the diagnostic body characters of the whole insect *Cretavus* would place it in the Aculeata or not.

The reason for the apparent absence of social insects before the Tertiary may be due at least in part to the general scarcity of Cretaceous insects. The most notable relevant Cretaceous deposit, the Cedar Lake amber from Manitoba studied by Carpenter and his associates (1934), contains moderate numbers of insects, and some are Hymenoptera, but these include no ants or aculeates of any kind. Two explanations seem possible: either the Cedar Lake amber, which has not been precisely dated within the Cretaceous,[3] originates from an early part of the period, prior to the origin of the aculeates, or else the early aculeates were too large to be enclosed in the small amber pieces that characterize the deposit. Amber has been found in Cretaceous deposits along the Arctic coastal plain of Alaska (Langenheim, Smiley and Gray, 1960) but very few insects are included and no aculeates have been reported.

For many years numerous pieces of amber have been recovered from sediments exposed along the coastal plain of Maryland and New Jersey, as well as on Staten Island and Nantucket. These pieces have apparently been derived from at least two formations, the Raritan and the Magothy, both of which are referable to the lower part of the Upper Cretaceous. The first published account of this amber appeared nearly 150 years ago (Troost, 1821) but, in spite of frequent observations on the occurrence of the amber, almost no records of insect inclusions have been published. Indeed, the only account of an inclusion was that in Troost's original report on the amber (1821), which contained a "description of a variety of amber and of a fossil substance supposed to be the nest of an insect".[4]

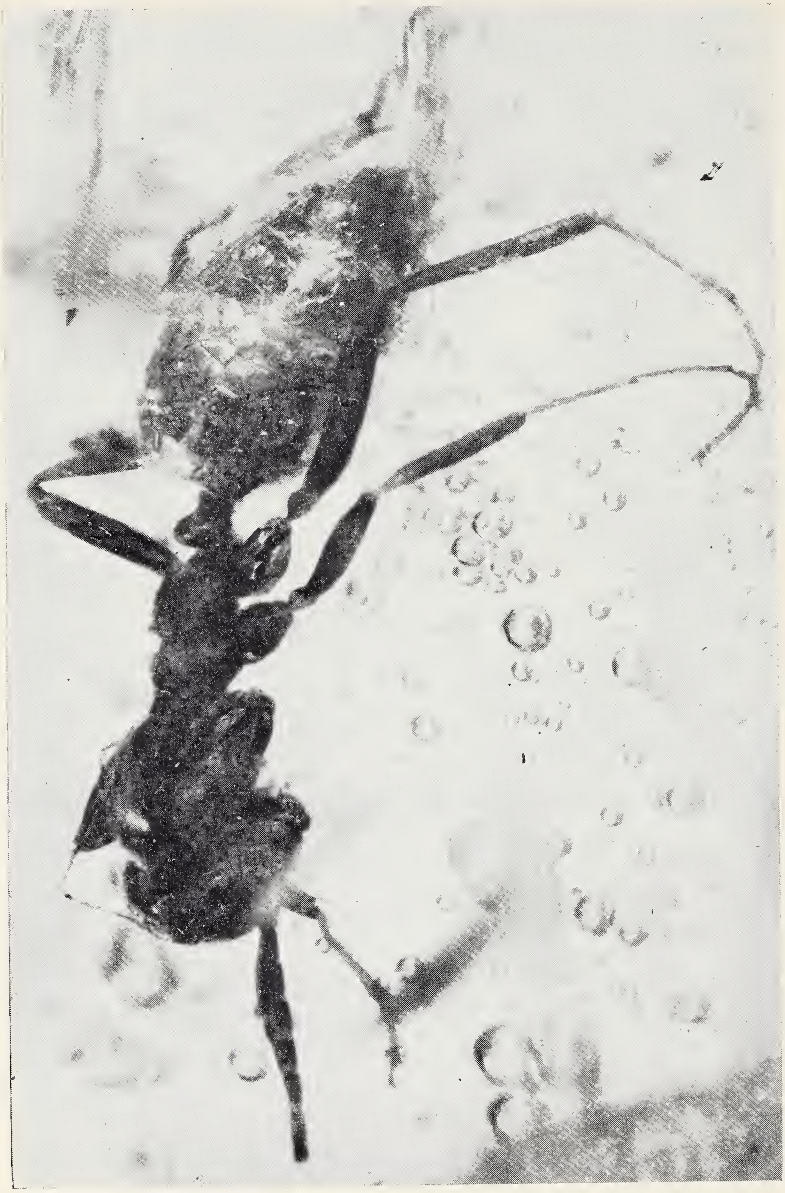
---

[3] Langenheim, Smiley and Gray (1960, p. 135) refer to the Cedar Lake amber as of "presumed Late Cretaceous Age". However, Dr. Langenheim informed me subsequently (pers. com., 1964) that he had no knowledge of evidence dating the amber at any specific level within the Cretaceous. [F. M. C.]

[4] It is of interest to note that at the first meeting of the Cambridge Entomological Club, January 4, 1874, Professor Hermann Hagen presented an account of this specimen, concluding that it was a group of galls on a twig (Hagen, 1874). No formal description was ever published.

EXPLANATION OF PLATE 2

Sphecomyrma freyi, worker no. 2, paratype. The head is viewed obliquely from below and in front.



Sphecomyrma freyi, worker no. 2, paratype.

In 1966 Mr. and Mrs. Edmund Frey, of Mountainside, New Jersey, while collecting mineralogical specimens in the Magothy exposure at the beach bluffs, Cliffwood, New Jersey, found a relatively large piece of amber containing several insects. The amber, when discovered, was imbedded in the clay bank. Professor Donald Baird of Princeton University reported the find to one of us (F.M.C.) and eventually Mr. David Stager of the Newark Museum kindly arranged for the loan of the specimen by Mr. and Mrs. Frey. All who are interested in insect evolution are indebted to Mr. and Mrs. Frey for their alertness in discovering the amber and especially for their full cooperation in allowing the amber inclusions to be prepared and studied. Important as these insects are, the knowledge that insects actually occur in this Cretaceous amber is of even greater significance. In all probability much of the amber previously collected contained insects that were simply not detected. Efforts are now being made to examine earlier collections of the amber from the Magothy and Raritan Formations and also to obtain new material by collecting at the several exposures of these two beds.

The Magothy Formation, in which this fossiliferous piece of amber was found, has exposures in Maryland, Delaware, New Jersey, Long Island and other islands of the southern New England coast. It consists mainly of light-colored sands, with layers of gray or dark brown clays. Leaf impressions, lignite and the amber occur in the clay beds. The Magothy Formation has been referred consistently to the lower part of the Upper Cretaceous (Turonian-Coniacian stages). Resting on the Raritan, which lies at the bottom of the Upper Cretaceous, it was presumably deposited not long after mid-Cretaceous times, about 100 million years ago. The plants in the Magothy Formation have been studied chiefly by Berry (1904, 1905, 1906, 1907) but his generic determinations are not generally accepted by botanists at the present time. More recently, pollen and spores in the Magothy have been investigated by Groot, Penny and Groot (1961) and by Stover (1964). Certain cones and twigs in the Magothy clays almost certainly belong to *Sequoia* (Berry, 1905; Hollick, 1905) or related genera. There is good evidence that such trees produced most of the amber now found in the Magothy. Knowlton (1896) reported that a lignitic log about 4 feet long, which was found in the Potomac Formation (below the Magothy, in the Lower Cretaceous) and which possessed a woody structure characteristic of *Sequoia,* contained several pieces of amber. Very recently (1967, pers. com.) Dr. Jean Langenheim, of the University of California at

Santa Cruz, has informed one of us (F.M.C.) that she has tentatively concluded from her infrared studies on resins and ambers that most of the Atlantic Coastal Plain amber (including that from Cliffwood beach) was probably produced by taxodiaceous trees, very likely *Sequoiadendron* or *Metasequoia*.[5]

Among the insects in the amber which Mr. and Mrs. Frey collected at Cliffwood beach are two unmistakable worker ants. These specimens have fulfilled many of our fondest speculations about what a Mesozoic ant might be like, and thus they demonstrate to us anew the predictive power of phylogenetic reasoning (See Plate 4). We first present their formal description as a new subfamily, genus, and species and then provide a discussion of their phylogenetic significance. The other insects in the amber, all Diptera, will be turned over to appropriate specialists for subsequent study and description.

Family Formicidae

Sphecomyrminae Wilson and Brown, new subfamily

Diagnosis (worker): Mandibles peculiarly wasp-like, short, narrow, curvilinear, bidentate. Antennae 12-segmented, with a well-formed but relatively short scape and an exceptionally long (for an ant), almost filiform funiculus. The second funicular segment is longer than any other funicular segment, a rather unusual feature apparently shared with *Nothomyrmecia* (some higher ants have a long second funicular fusion segment, e.g., workers and females of *Orectognathus* and males of most *Tetramorium* and allied genera). Compound eyes large, convex, placed near the middle of the sides of the head. Ocelli present.

Body form that of a very primitive formicid. Alitrunk (=thorax + propodeum) slender, in form very much like that of *Methocha malayana* (Fig. 3), *M. stygia,* and some other species of that genus (Reid, 1941: figs. 26-27; Pagden, 1949). Sutures between pro- and mesothorax, and between meso- and metathorax, both complete, possibly movable. Mesonotom long and slender, with distinct, convex scutum and scutellum separated by a rather distinct axillary region. Metathoracic spiracles present, situated just below the limits of the scutellum on each side near its posterior margin, as in

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[5] We are indebted to Mr. James Doyle of Harvard University for his assistance with this paleobotanical literature.

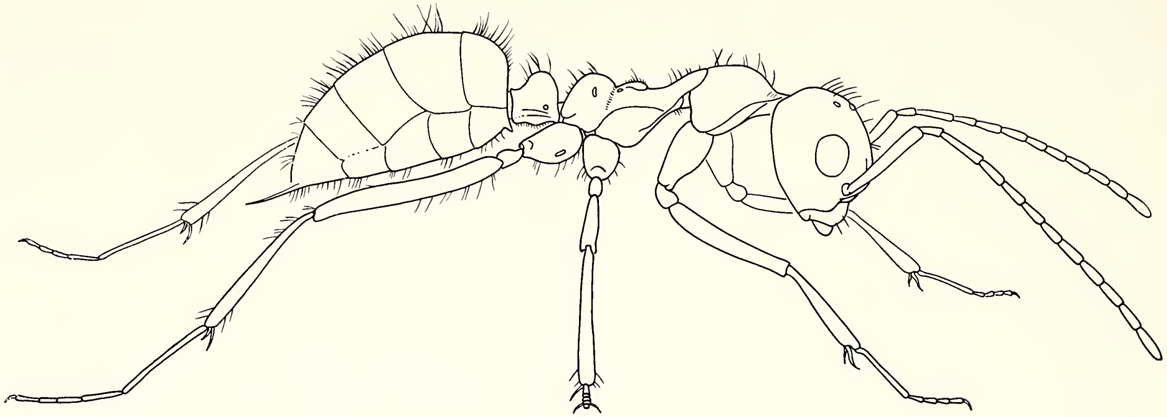


Figure 1. Drawing of *Sphecomyrma freyi,* worker no. 1. Only structures that could be clearly seen were drawn. Thus the figure is a direct rendition and not a reconstruction, although the appendages have been turned to more life-like positions.

Methocha. Metanotum a deeply impressed transverse groove between scutellum and rounded propodeum. Metapleural gland bulla and meatus present and well-developed (though it is difficult to be absolutely certain of this in amber specimens). Petiole with a distinct, raised node with strongly rounded summit, strongly separated from propodeum and first segment of gaster by deep constrictions. Gaster without a constriction behind first segment; strong exsertile sting present. Legs long and slender, the last two pairs having 2 spurs at the apex of each tibia. Tarsal claws each with a median tooth. Type and only known genus is the following:

Sphecomyrma Wilson and Brown, new genus

Worker: With the characters of the subfamily. Head capsule unexceptional, more or less like that of a primitive formicine, such as *Prolasius, Notoncus,* or even *Prenolepis.* Clypeus broad, simply formed, convex, with broadly rounded free margin. Antennae inserted moderately far apart and well forward on the head capsule, their sockets close to the posterior margin of the clypeus. Compound eyes oblate circular in outline, large and convex, each with more than 100 ommatidia. Ocelli well-developed. Antennal segmentation and proportions unique, as shown in Figure 2A.

Alitrunk with rounded humeri. Propodeal spiracle high up, its opening elongate. Petiolar segment with a distinct node in the form of a narrowly-rounded dome, briefly pedunculate in front and behind, much narrower than the succeeding (gastric) segment, and separated from it by a broad and deep constriction. First gastric segment with an anteroventral process like that found in *Myrmecia* as well as many ponerine genera. Sting exserted, strong and acute.

Integument appearing relatively thin, not boldly sculptured anywhere; sculpture fine and superficial, body surface opaque to subopaque.

Queen and male unknown.

Type and only known species: *Sphecomyrma freyi,* described below.

Sphecomyrma freyi Wilson and Brown, new species

Plates 1-4; Figures 1, 2

Holotype and paratype workers: the characters cited in the subfamily diagnosis, and particularly the form of the mandibles, antennae and mesonotum, readily distinguish this species from all other known ant species, living or fossil.

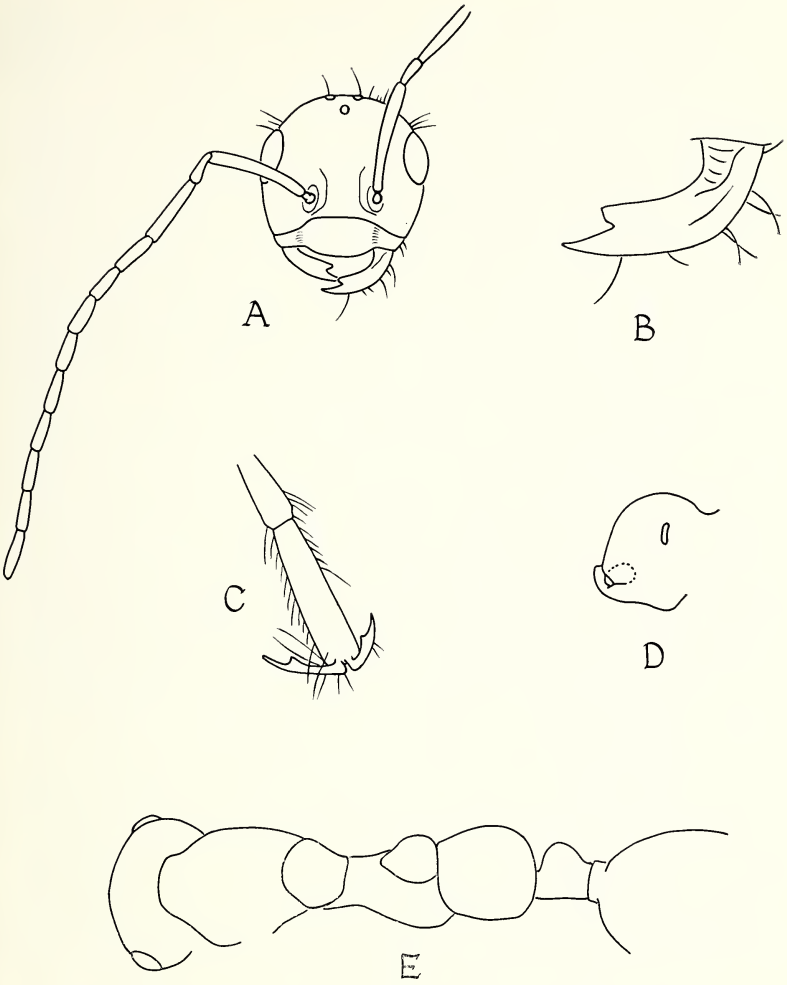


Figure 2. Drawings of various body parts of *Sphecomyrma freyi.* A, head of worker no. 2, view from below and in front. B, left mandible of worker no. 2, seen in fuller frontal view than in A so as to reveal the truncated shape of the inner tooth. C, pretarsus of left hind leg of worker no. 1. D, propodeum and metapleural region of worker no. 1. E, oblique dorsal view of body of worker no. 2.

The two workers are very similar in most characters, but differ markedly in size. Both are roughly what would be called "medium-sized" ants. Some exact measurements could be taken, to the nearest 0.01 mm, and these are given in millimeters as follows:

Specimen 1. Head width not measured; head length along mid-line 0.98; maximum length of right eye 0.32. Segments of left antenna (numbered I through XII) from insertion outward: I (scape) 0.60, II 0.16, III 0.34, IV 0.21, V 0.21, VI 0.21, VII 0.21, VIII 0.21, IX 0.21, X 0.21, XI 0.21, XII 0.26. (Holotype).

Specimen 2. Head width taken just anterior to the compound eyes, 1.00; head length not measured. Segments of right antenna (numbered I through XII) from insertion outward: I (scape) 0.68, II 0.18, III 0.40, IV 0.27, V 0.27, VI 0.26, VII 0.26, VIII 0.26, IX 0.24, X 0.23, XI 0.23, XII 0.31. (Paratype).

The details of morphology, including pilosity, are evident in the figures. Pubescence consists of scattered, short (about 0.01 mm long), appressed hairs. Both specimens are uniform light brown in color, but this means little in view of the passage of 100 million years.

Holotype: worker, labelled F1, shown in photograph, Plate 1; paratype: worker, labelled F2, shown in photograph, Plate 3. Both specimens were collected in a single piece of amber (now in seprate pieces) in clay, Cliffwood Beach, on Raritan Bay, New Jersey, by Mr. and Mrs. Edmund Frey. The specimens are in the collection of Mr. and Mrs. Frey, Mountainside, New Jersey.

PHYLOGENETIC POSITION OF SPHECOMYRMA

Sphecomyrma freyi presents a mosaic of wasp-like and ant-like character states. Moreover, most of the ant-like features are, as well as we can judge the matter, primitive with respect to the other known Formicidae. Our assignments of various character states are given in Table 1. An examination of this arrangement will show that *Sphecomyrma* is truly intermediate between the primitive ants

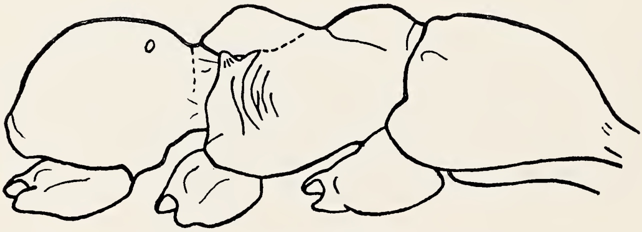


Figure 3. Alitrunk of *Methocha malayana* female in side view. (Redrawn after Pagden, 1949).

and the aculeate wasps. However, we feel that the metapleural gland, the nodiform, posteriorly constricted petiole, and the generally ant-like overall habitus place this species among the primitive ants rather than the wasps. However, if we are mistaken about the presence of the metapleural gland, it would be possible to consider *Sphecomyrma* as a wasp rather than an ant.

Which of the aculeate wasp groups might have given rise to the Sphecomyrminae? In Table 2 we present a scheme by Dr. Howard E. Evans, who has compared the Mesozoic ant with a wide range of modern aculeate families (fossil wasps are too scarce to be of much use). It can be seen that the Tiphiidae, and in particular the genus *Methocha*, come closest. (*Methocha* is impressively similar in details of thoracic structure, as shown in Figure 3). But we agree with Evans that such a comparison must be treated very carefully. The modern aculeate wasps are specialized both morphologically and ecologically: for example, *Methocha* of several species are known to

TABLE 1

Relationships of the Principal Character States of *Sphecomyrma freyi*

	Aculeate wasps only	Other primitive ants only	Both aculeate wasps and primitive ants
Narrow bidentate mandibles	+		
Well-formed slender scapes		+	
Long, filiform funiculi	+		
Large compound eyes			+
Well-formed ocelli			+
Broad, simple clypeus			+
Reduced, apterous thorax			+
Mesonotum with separate, distinctly convex scutum and scutellum	+		
Metapleural gland		+	
Petiole with node deeply constricted front and rear		+	
Gaster ovoid, unconstricted			+
Extrusible sting			+

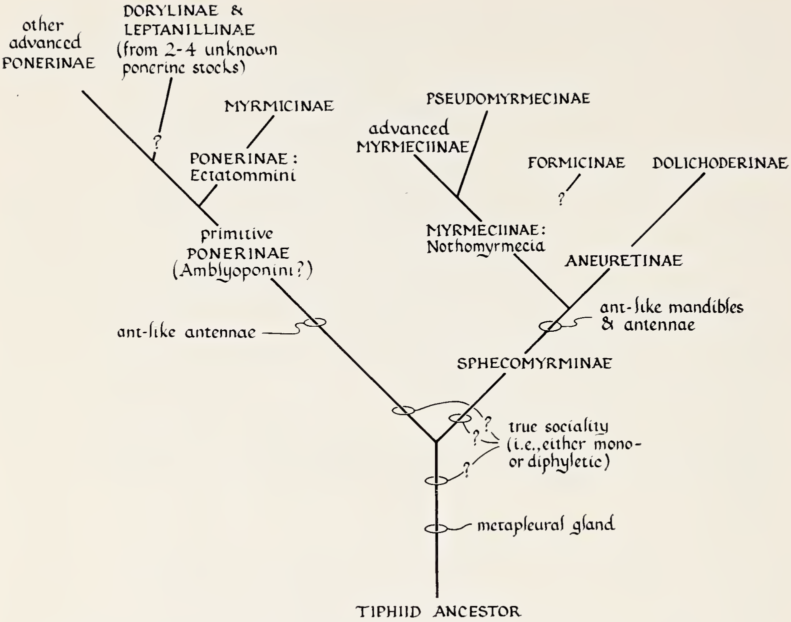

other advanced PONERINAE
DORYLINAE & LEPTANILLINAE (from 2-4 unknown ponerine stocks)
?
MYRMICINAE
PONERINAE: Ectatommini
primitive PONERINAE (Amblyoponini?)
PSEUDOMYRMECINAE
advanced MYRMECIINAE
FORMICINAE
DOLICHODERINAE
?
MYRMECIINAE: Nothomyrmecia
ANEURETINAE
ant-like mandibles & antennae
ant-like antennae
SPHECOMYRMINAE
true sociality (i.e., either mono- or diphyletic)
?
?
?
?
metapleural gland
TIPHIID ANCESTOR

Figure 4. Hypothetical cladogram of the subfamilies of ants (Formicidae), based on all available evidence including the analysis of *Sphecomyrma.*

be parasitoids of tiger beetle larvae (Clausen, 1940: 298). There is now a greater need than ever to discover and to study in detail aculeate wasps of Cretaceous age.

The relationship of *Sphecomyrma freyi* to the other ants is clearer. The body of *Sphecomyrma* resembles that of the primitive myrmecioid ants, notably the living *Nothomyrmecia macrops* of Australia, which we regard as the most generalized member of the primitive subfamily Myrmeciinae (Brown and Wilson, 1958), and the Eocene genera of Aneuretini, which are the undoubted ancestors of the other Dolichoderinae (Wilson *et al,* 1956). Previously we had considered that the Aneuretini might have been derived from the Myrmeciinae, because we considered the long mandibles of the Myrmeciinae as primitive and the short mandibles of the Aneuretini as derived. Now the discovery of short, wasp-like mandibles in *Sphecomyrma* has invalidated this postulate.

In *Sphecomyrma,* then, we have what appears to be a good link between aculeate wasps and the myrmecioid complex of subfamilies,

Table 2. Degree of similarity of body parts of *Sphecomyrma freyi* with genera of various aculeate families. +++, nearly identical, scored as 3. ++, mostly similar, with minor differences, scored as 2. +, mostly dissimilar but with a few details matching, scored as 1. —, wholly dissimilar, scored as 0. These genera include those previously believed to fall closest to the primitive ants, as well as other, representative genera. Except for the Oligocene *Paraneuretus*, all are represented by living species. (The evaluation of the wasp families was provided by Dr. Howard E. Evans.)

	Mandibles	Clypeus	Antenna	Ocelli	Petiole	Alitrunk (Mesosoma)	Similarity to *Sphecomyrma* numerical score
POMPILIDAE							
Epipompilus ♀	+++	+	++	++	—	—	8
SIEROLOMORPHIDAE							
Sierolomorpha ♀	+	++	++	++	+	—	8
RHOPALOSOMATIDAE							
Rhopalosoma ♀	—	—	+	+	+	—	3
PLUMARIIDAE							
Plumarius ♀	—	—	—	—	—	—	0
Plumarius ♂	—	+	+	+	—	—	3
MUTILLIDAE							
Apterogyna ♀	—	—	++	—	++	—	4
Apterogyna ♂	—	++	+	++	++	—	7
VESPIDAE							
Gayella ♀	—	+	+	++	++	—	6
Alastor ♀	—	++	+	++	+	—	6
THYNNIDAE							
Aelurus ♀	—	—	—	—	—	—	0
Aelurus ♂	++	++	+	++	—	—	7
Diamma ♀	—	+	—	++	+	+	5
Diamma ♂	—	++	+	++	+	—	6
Rhagigaster ♀	++	+	—	—	—	—	3
Rhagigaster ♂	+++	++	++	++	+	—	10
TIPHIIDAE							
Anthobosca ♀	—	++	—	++	—	—	4
Anthobosca ♂	+++	++	+	++	—	—	8
Glyptometopa ♀	—	—	—	—	—	—	0
Methocha ♀	+++	++	++	++	—	+	10
FORMICIDAE							
Amblyopone ♀	—	++	++	—	+	++	7
Nothomyrmecia ♀	+	+++	++	++	++	+++	13
Paraneuretus ♀	++	+++	++	—	++	+++	12

namely the Myrmeciinae, Pseudomyrmecinae, Dolichoderinae (including Aneuretini) and Formicinae. (See the arrangement of ant subfamilies into the "myrmecioid" and "poneroid" complexes by Brown, 1954). Where does this leave the poneroid subfamilies in the scheme of things? Among the poneroids, including the Ponerinae, Dorylinae, Leptanillinae, and Myrmicinae, the most primitive group is certainly the Ponerinae, and most particularly the ponerine tribe Amblyoponini. It is disconcerting to find that the ponerines are hardly closer to *Sphecomyrma* than they are to the primitive myrmecioids. There is no trace of the ponerine gastric constriction in the latter two groups. More significantly, the Amblyoponini have an incompletely constricted petiole (that is, the petiole is broadly attached posteriorly to the gaster), and they *also* have the constriction between the first and second gastric segments. *Sphecomyrma* lacks the gastric constriction, but has the petiole strongly constricted behind. We have long considered the amblyoponine petiolar form as primitive among the ants, and it certainly resembles that of some tiphioids as much as or more than it does that of most other ants.

One character that has never received any particular attention is the form of the amblyoponine male mandibles (Brown, 1960: figs. 8, 26) which is in fact now seen to be quite primitive. In the species of Amblyoponini so far described, the mandibles are narrow and wasp-like, sometimes bidentate, and sometimes tapering to a single acute point (the latter condition is evidently derived); they close tightly against the convex free clypeal margin, as do those of most wasps. (The more elaborate worker-female mandibles of Amblyoponini are not too difficult to imagine as derived from the bidentate wasp-like form.) When considered together, the petiole and the male mandibles of Amblyoponini certainly strengthen the general impression that this tribe is very primitive, although it shows tendencies toward specialization for life in cryptic habtats.

If the amblyoponine petiole is truly more primitive than the *Sphecomyrma* petiole, then the split between myrmecioids and poneroids must have come at a time when ants were still very wasp-like, and perhaps we should even consider the possibility that the divergence occurred before these groups had fully acquired their sociality. In the light of this last possibility, the metapleural glands assume a particular importance in our phylogenetic speculations. The fact that they are such complicated organs makes it unlikely that they were evolved independently in different ant lineages. If their function — at present unknown — is eventually shown to be primarily social, then the hypothesis of a single origin of social life in ants would tend to be supported.

A cladogram outlining our present best guess at ant phylogeny is given in Figure 4.

RECONSTRUCTION OF FORMICID ARCHETYPE

Judging from the characteristics of the primitive ants and the tiphiid wasps as we know them now, we would reconstruct the archetypal ant as follows:

Worker —

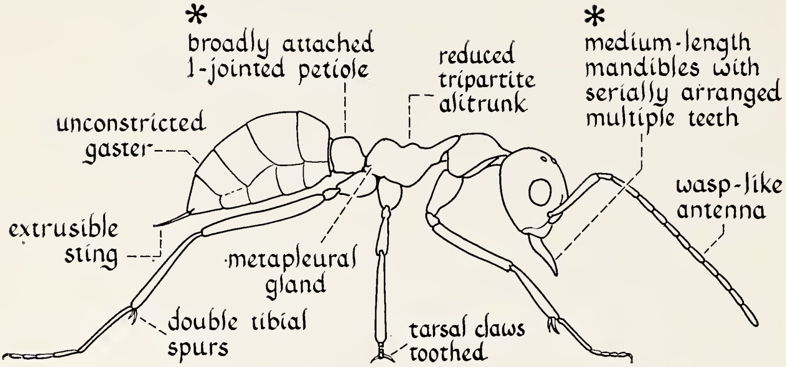
1. Mandibles narrow, short, curved, bidentate, closing tightly against clypeus.
2. Maxillary palpi 6-segmented, labial palpi 4-segmented.
3. Antennal scapes shorter than in most ants, but a little longer and more slender than in most tiphiids.
4. Antennal funiculi long, slender, filiform, with 11 segments.
5. Compound eyes large, convex, oval or round, situated near middle of sides of head.
6. Ocelli well-developed.
7. Promesonotal suture complete, movable.
8. Mesonotum with scutum and scutellum separate and distinct.
9. Mesonoto-metanotal suture complete, possibly movable.
10. Metapleural gland bulla and meatus present.
11. Tibial spurs 1, 2, 2.
12. Tarsal claws toothed.
13. Petiole consisting of a single segment, sessile in front, or nearly so, sessile and broadly joined to gaster behind (with little intervening constriction).
14. Gaster unconstricted.
15. Sting strong and functional.

Of these character states, *Sphecomyrma* agrees with all but No. 13 (petiole form); its status with regard to No. 2 (palpal segmentation) is actually unknown, but we would strongly expect it to agree.

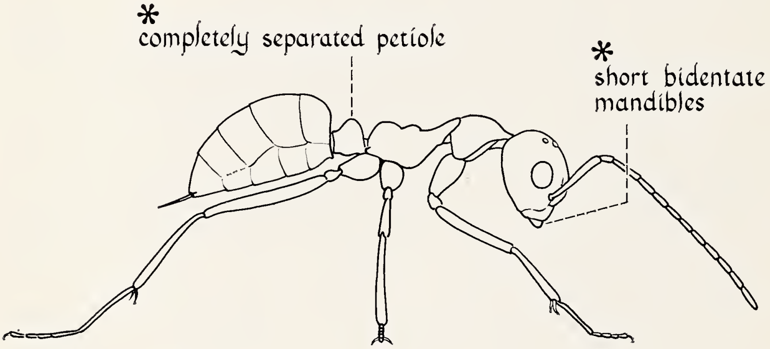
The primitive *Amblyopone* species have workers agreeing with the archetype more or less closely in character Nos. 3, 7, 10, 11, 13 and 15. Males of the larger and more primitive species of *Amblyopone* also agree in No. 1.

The *Nothomyrmecia macrops* worker agrees with Nos. 2, 4 (more or less), 5, 7, 10, 11, 12, 14 and 15.

The *Methocha stygia* female agrees well to fairly well with all character states except 10 and 12.



PREVIOUSLY HYPOTHESIZED ANCESTOR



SPHECOMYRMA

Our analysis of *Sphecomyrma*, incomplete as it must be, nevertheless suggests several promising lines of investigation in the future. First and foremost, of course, is the search for more Cretaceous ants and allied aculeate groups. Perhaps the Magothy amber will yield more material of interest. Second, we should pay closer attention in the future to comparisons in morphology, physiology, and behavior between the primitive myrmecioids and primitive poneroids. Differences should be related to the emerging new form of the formicid cladogram, while similarities should be examined with reference to the question of whether they are monophyletic or convergent. Finally, as a better idea is formed of the relationships of the ants to certain living wasp families, the biology of the latter needs to be examined more closely for clues concerning the origin of social life in ants.

ACKNOWLEDGEMENTS

We gratefully acknowledge the splendid cooperation of Mr. and Mrs. Edmund Frey, as well as the intermediary aid of Dr. Donald Baird of Princeton University and Mr. David Stager of the Newark Museum. Our separate research programs, within which the analysis of *Sphecomyrma* was undertaken cooperatively, have been supported by grants from the National Science Foundation: NSF GB-5574X (Brown), NSF GB-2038 (Carpenter), and NSF GB-1634 (Wilson).

SUMMARY

Two worker ants preserved in amber of Upper Cretaceous age (Magothy Formation) have been found in New Jersey. They are the first undisputed social insect remains of Mesozoic age, and extend the existence of social life in insects back to approximately 100 million years. They are also the earliest known, certainly assignable aculeate Hymenoptera. The species, *Sphecomyrma freyi*, is considered to

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EXPLANATION OF PLATE 4

A comparison of the archetypal ant as hypothesized by the authors before the discovery of *Sphecomyrma* (e.g., Brown, 1954; Brown and Wilson, 1959), with *Sphecomyrma* itself. The fine details of body shape are made the same in this drawing for convenience but do not enter into the main features to which phylogenetic speculation has been directed. This comparison is presented to indicate the degree of precision of earlier phylogenetic reasoning. Examination of the *Sphecomyrma* specimens proved the hypothesis wrong in essentially only one major respect: we had guessed that an ant-like mandible developed before an ant-like petiole, but the reverse proved to be the case.

represent a new subfamily *(Sphecomyrminae)* more primitive than any previously known ant group. It forms a near-perfect link between certain non-social tiphiid wasps and the most primitive myrmecioid ants.

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ANATEA, AN ANT-MIMICKING THERIDIID SPIDER FROM NEW CALEDONIA (ARANEAE: THERIDIIDAE)

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The morphological and behavioral adaptations necessary for ant mimicry have arisen independently many, many times in spiders. Ant mimicry has originated at least four times in the Clubionidae, three times in the Salticidae, several times in the Theridiidae, Araneidae and Thomisidae, and also in the Gnaphosidae, Zodariidae and Eresidae. In addition the bizarre characteristics of these spiders have led spider specialists to group some of the stranger species into families — such as the Myrmecidae C. L. Koch 1851 (mainly including ant-mimicking genera from the Micariinae of the Clubionidae) and the Aphantochilidae (a group of highly modified Thomisidae that mimic cephalotine ants). Walckenaer (1841) included in the genus *Myrmecia* members of both the Clubionidae and the Salticidae, all good myrmecomorphs. This tendency to be biased by the outward modifications associated with ant mimicry resulted in the placing of *Anatea formicaria* Berland in the sub-family Micariinae (Clubionidae) when it was first described (Berland, 1927). Berland based his placement on general shape and male genitalia. The latter resembles the male genitalia of *Micaria*, but only in that both are quite simple and have a central sclerotized process.

Anatea formicaria Berland should be in the family Theridiidae. Closely related to *Euryopis* and possibly to *Achaearanea*, it lacks a colulus and has toothless cheliceral margins. The palpus, which lacks a radix, is simpler than in either *Euryopis* or *Achaearanea* but is definitely related. As in some *Euryopis* the abdomen is sclerotized with scuta and the chelicerae are very small with huge sickle-shaped fangs, possibly indicating that *Anatea* feeds on ants as do members of *Euryopis* and related *Dipoena*. The function of the sickle-shaped fang is not known although the unusual method used to catch ants by *Euryopis flavomaculata* C. L. Koch has been observed (D. Hirschberg in manuscr.). While it is unlikely that the mimicry would deceive an ant, the occurrence of the spider near the ants (a prey-predator relationship) could account for strong selection pressure applied by predators of the spider.

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There are four or five other known theridiid ant mimics: *Cerocida strigosa* Simon, *Helvibis brasiliana* (Keyserling) and *H. chilensis* (Keyserling), the male of *Coleosoma floridanum* Banks, and perhaps *Hetschkia gracilis* Keyserling. All except the *Coleosoma* create the impression of a petiole by a posterior elongation of the cephalothorax, most highly perfected in *Cerocida* where the "petiole" is rugose and sharply delimited from the rest of the carapace. *Coleosoma floridanum* has a highly constricted abdomen. But in *Coleosoma* only the males resemble ants, the females are characteristic sedentary theridiids hanging in a web.

Anatea formicaria, unlike any other theridiid, produces its "petiole" by an elongation of the pedicel. In addition the dorsum of the "petiole" is rugose and has a distinct "node" as is typical in most ants. The abdomen is globose and highly shiny — very much like an ant's gaster.

Anatea formicaria is an accurate mimic of the small myrmicine ant *Chelaner croceiventre* (Emery), 2.6 mm long, which has been collected at the same locality as the spider. The color pattern (dark brown anterior and light, yellow-brown posterior) of both is quite rare in ants and is also found in specimens of *Xiphomyrma tenuierius* Emery, 2.9 mm long, and a species of *Lordomyrma,* 4.8 mm long, two myrmicine ants found in the same area of rain forest (E. O. Wilson, pers. comm.). Myrmicine ants have large and well-developed stings and are therefore quite objectionable to most potential predators. Such a pattern may represent a mimetic complex with the ants being Müllerian mimics and the spider a Batesian mimic of one or more ants.

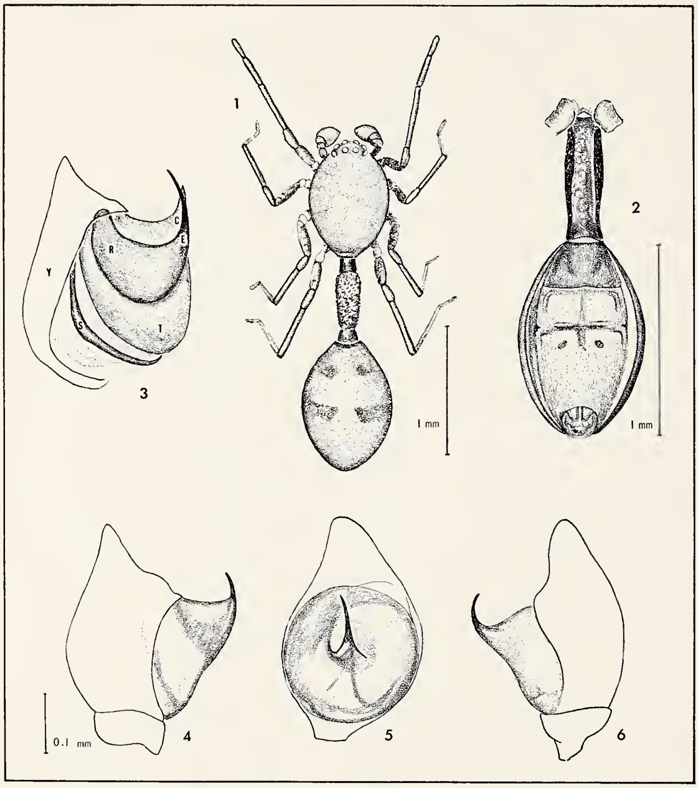
The genus *Anatea* will presumably key out to *Euryopis* in the key to theridiid genera (Levi and Levi 1962) but differs from *Euryopis* in having a simpler palpus (Figs. 3-6) and from all theridiid genera in the extraordinary development of the pedicel, and the strong first legs. Berland indicates that the female resembles the male.

Anatea formicaria Berland 1927

Figs. 1-6

Description: Male. Carapace, sternum brown and sclerotized, legs lighter brown. Dorsum of abdomen light brown with four darker areas and a polished, shiny surface. Eyes subequal in size. Anterior median eyes about one-half diameter apart, a little more than one diameter from laterals. Posterior median eyes their radius apart, one and one-quarter diameters from laterals. The pedicel is unusually long with a joint at each end. The chelicerae are weak with fang longer than basal segment. Abdomen has a dorsal shield wrapped around it, partly covering venter (Figs. 1, 2). Tracheal spiracle far anterior (Fig. 2). Legs almost equal in length; first tarsi and metatarsi thicker than tibiae. Tarsal comb on fourth legs reduced or absent. Total length 2.5 mm. Carapace 0.84 mm; pedicel 0.62 mm; abdomen 1.04 mm long. First femur, 0.63 mm; patella and tibia, 0.67 mm; metatarsus, 0.36 mm; tarsus, 0.28 mm. Second patella and tibia, 0.63 mm; third patella and tibia, 0.60 mm. Fourth femur, 0.63 mm; patella and tibia, 0.75 mm; metatarsus, 0.42 mm; tarsus, 0.34 mm.

The palpus is very simple (Fig. 3-6). Using the nomenclature of palpal sclerites used in the theridiid revisions, the median apophysis



Figs. 1-6. *Anatea formicaria* Berland. Fig. 1. Dorsal view of male. Fig. 2. Ventral view of pedicel and abdomen. Figs. 3-6. Left palpus. 3. Expanded, mesoventral view. 4. Mesal view. 5. Ventral view. 6. Ectal view. *Abbreviations.* C, conductor; E, embolus; S, subtegulum; T, tegulum; Y, cymbium.

is broadly joined to the embolus and the radix is absent. (It has since been found that the "radix" of theridiid spiders is homologous to the median apophysis of araneid spiders and the "median apophysis" to the radix).

Record: Male from rainforest at Ciu, near Mt. Canala, 300 m, New Caledonia, 31 Dec. 1954 — 1 Jan. 1955 (E. O. Wilson) in the Museum of Comparative Zoology.

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CAVE CARABIDAE (COLEOPTERA) OF MAMMOTH CAVE, PART II.

By Thomas C. Barr, Jr.

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This is a continuation of my account of the Cave Carabidae of Mammoth Cave, the first part of which was published in the preceding issue of Psyche (Volume 73, pp. 284-287).*

P. inexpectatus forms the type of an *inexpectatus* species group, generally distributed eastward and northward from Mammoth Cave. The species are all rather small (less than 4 mm) and slender, with unusually elongate, slender aedeagi containing long, slender copulatory pieces. The posterior margin of the last sternite in the males is broken by a distinct notch. The affinities of the *inexpectatus* group seem to lie with *P. gracilis* Valentine (Giles Co., Virginia), *P. hadenoecus* Barr (Pendleton Co., West Virginia), and undescribed species from Fayette Co., Pennsylvania, and Randolph Co., West Virginia. All of these eastern species are small, have an elongate aedeagus, reflexed at the tip, and have the last sternite of the males notched. The copulatory pieces are considerably shorter, however, than those of the *inexpectatus* group. In *P. horni* and related species in the inner Bluegrass of Kentucky there is a slight emargination in the last sternite of the males. Perhaps this indicates an affinity with the *inexpectatus* group, but the single copulatory sclerite and other morphological characters suggest that *horni* and its relatives are more closely allied with the *audax* group.

P. pubescens has been taken sporadically at two sites in Mammoth Cave: (1) Crevice Pit, near the top of Mammoth Dome; and (2) on cave cricket guano near the top of Moonlight Dome in the Frozen Niagara part of the cave. Elsewhere in Mammoth Cave National Park it has been collected in one of two caves in the bottom of Cedar Sink, 4 miles southwest of the Historic Entrance to Mammoth Cave. *P. pubescens* occurs frequently along cave streams, but is not uncommon in certain caves in rather dry areas, where it occurs crawling about on dry silt in the manner of *Neaphaenops*. It does not appear to show as narrow a degree of habitat selection as *mene-*

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*As a result of a printing error, this part of Professor Barr's article was omitted from his account of the Mammoth Cave Carabidae in the December, 1966, issue of Psyche (pp. 284-287). Since this omission was not discovered until after the copies of the issue had been mailed, the rest of the paper is published here as a continuation of the previous article. [Editor].

triesii and *striatus*, and is possibly a more generalized predator. The *pubescens* group ranges south and west from Mammoth Cave and the *menetriesii* group ranges north and east, although the two groups overlap broadly in Edmonson, Hart, Warren, and Barren counties near Mammoth Cave. The two groups are probably distantly related because of the unusual, anterior position of the first discal seta, but the shape of the aedeagus and the structure of the transfer apparatus is quite different in each group.

With these 6 rather closely related species, the Mammoth Cave system has the most diverse trechine fauna of any cave in North America. Sympatry of 2, 3, or even 4 species is not uncommon in certain caves of the Greenbrier Valley of West Virginia or the western margin of the Cumberland plateau in Tennessee and Kentucky. Perhaps more species would be discovered in some of these other caves if they were subjected to the same intensive collecting that Mammoth Cave has enjoyed over the past 125 years. Despite this attention, it is worth noting that *P. inexpectatus* was not discovered in Mammoth Cave until 1957, and that *P. audax* has been taken only 3 times in 85 years.

The presence of 6 similar species in the same cave leads naturally to consideration of the principle of competitive exclusion, according to which these species should occupy different niches. From what has already been said about the habitat preferences of *P. striatus* and *P. menetriesii* — the two most closely related species — it seems clear that their niches quite probably overlap but include significant, mutually exclusive components. *P. pubescens* probably bears a similar relationship to each of these two species, since the three coexist syntopically not only in Mammoth Cave but also in Diamond Caverns, Cave City Cave, Walnut Hill Cave, and in various other caves of the Pennyroyal plateau. Its relative rarity in Mammoth Cave has yet to be explained. *Neaphaenops tellkampfii* feeds heavily on the eggs and nymphs of the cave cricket, *Hadenoecus subterraneus* (Scudder), although it is not limited to this food. To its exploitation of a food not generally utilized by other trechines may be atributed its occurrence in drier upper galleries, its extraordinary abundance and greater size, its extensive geographical distrivution, and its sympatry in various parts of its range with no less than 10 species of *Pseudanophthalmus*. The peculiar, seasonal occurrence of *P. inexpectatus* (late winter and early spring) and *P. audax* (late summer), and their great rarity could mean that they occupy unusual, as yet unsuspected niches, or that they compete less successfully for the resources of the environment with the other species.

Acknowledgments: I wish to thank M. S. Ghilarov and K. V. Arnoldi for checking the Motschulsky types in the Zoological Museum of Moscow, T. G. Marsh and R. M. Norton for assistance in collecting, and Superintendent Paul McG. Miller for permission to collect in Mammoth Cave National Park.

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A NEW SPECIES OF *TRACHYSPHYRUS* FROM THE ANDES OF ECUADOR (HYMENOPTERA, ICHNEUMONIDAE)

By Charles C. Porter
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The author has just completed a revision of the South American species of the otherwise primarily Holarctic ichneumonid genus *Trachysphyrus* Haliday. This monograph is scheduled to be published before the end of 1967 by the American Entomological Institute. Although nearly 100 species are there treated, collections from much of South America are so inadequate that the discovery of many additional forms is to be anticipated. Indeed, several more species have come to the author's attention after the acceptance of his manuscript for publication. Some of these are represented by single specimens and their description seems best postponed until larger series are obtained. The species treated here, however, is available in sufficient numbers to make possible a complete and reliable diagnosis and is also interesting as the second member of its genus to be described from the very poorly known Ecuadorian fauna.

Trachysphyrus hoplites n. sp.

Figures 1, 2. Map 1.

Types: *Holotype:* (female) ECUADOR (Cerro Tinajillas, 3200 m., March 18-21, 1965, L.E. Peña) (Townes). Paratypes: (1 female and 6 males). ECUADOR (Cerro Tinajillas, 3200 m., March 18-21, 1965, L.E. Peña; Targui,[1] 2800 m., March 7-8, 1965, L.E. Peña) (Cambridge, Porter, Townes).

Female: *Color:* antenna blackish with a white band, or sometimes only dull brownish staining, above on flagellomeres 5-9; head, thorax, and propodeum black with white markings as follows: dull patch just above mandibular condyle; sometimes tiny spot in middle of face below antennal sockets; orbital line: more or less interrupted on bottom of eye, on about lower ¼ of hind-orbit, and sometimes irregularly near top of eye; transverse blotch on collar; narrow line, fragmented to practically complete, on latero-dorsal margin of pro-

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[1] There is no such locality in atlases and gazetteers available to me. Probably this is a misspelling of *Tarqui,* a village in the same part of Ecuador as Cerro de Tinajillas.

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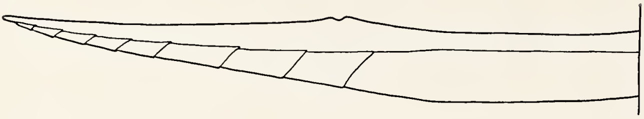
notum; spot or blotch on subalarum; and pair of small spots on base of scutellum; gaster pale orange; legs black, slightly brownish-stained especially on tarsi; wings vaguely darkened, particularly toward apex. *Length of fore-wing:* 7.0-7.4 mm. *Flagellum:* rather stout, slightly flattened below toward apex, 1st segment 5.0-5.7 times as long as deep apically. *Clypeus:* high, more or less symmetrically convex to bluntly subpyramidal in profile; apical margin almost truncate to gently convex, unusually sharp and a little reflexed especially toward corners. *Malar space:* 1.2-1.3 times as long as basal width of mandible. *Temple:* 0.4-0.5 times as long as eye in dorsal view; strongly, directly receding. *Genal and Oral Carinae:* genal carina sharp and narrow, joining the moderately elevated oral carina below. *Fore-tibia:* not inflated. *Pronotum:* submarginal groove distinct but rather narrow and shallow; epomia strong in scrobe, continued, usually more irregularly, a subequal or greater distance below, often gently traceable mesad above but without a definite swelling above its upper end. *Mesoscutum:* notauli narrow and shallow, traceable about ½ the length of mesoscutum; surface largely mat, granularly puncto-reticulate: dullest with more distinct small, shallow punctures and intercalated micro-reticulation toward centers of lobes; more nearly shining and with stronger wrinkling along notauli, over a broad area behind their terminus, and on peripheries of lateral lobes. *Mesopleuron:* subalarum an unusually thin, crescentic lamella; speculum swollen and shining but often much invaded by strong



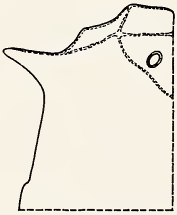
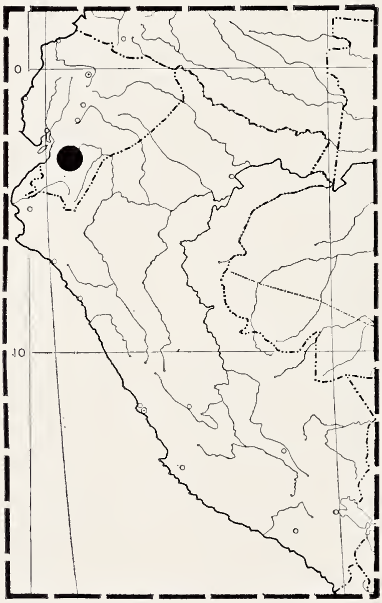


Fig. 1. *Trachysphyrus hoplites* n. sp. female. Lateral view of apex of ovipositor.

Fig. 2. *Trachysphyrus hoplites* n. sp. female. Lateral view of propodeum.

punctures and wrinkles; surface otherwise with rather coarse reticulate wrinkling. *Wing-Venation:* radial cell 3.8-4.1 times as long as wide; areolet large, intercubiti strongly convergent above, 2nd abscissa of radius 0.7-0.8 times as long as 1st intercubitus; 2nd recurrent slightly inclivous or nearly vertical, gently and almost evenly outcurved or more strongly curved on upper ½; disco-cubitus broadly angled, without or with a short to moderately long ramellus; nervulus a little antefurcal to interstitial; mediella gently arched throughout; upper part of nervellus 1.6-1.7 times as long as lower; axillus close to hind-margin of wing. *Propodeum:* short and high, faces subequal: basal moderately sloping behind, apical almost vertically declivous; spiracle 1.2-1.3 times as long as wide; basal trans-carina sharp throughout, in places a little irregular, strongest and forming low-crescentic or subcuneate cristae laterad; apical trans-carina detectable but very irregular, especially medially; cristae of apical trans-carina exceptionally large and strongly projecting ligulate; median longitudinal carinae vague or weak and irregular, areola definitely wider than long in position; lateral longitudinal carinae irregularly traceable basad, becoming stronger between trans-carinae and, especially, as they continue onto cristae behind; surface strongly reticulately wrinkled, a little more weakly sculptured basad of basal trans-carina. *1st gastric segment:* no expansion at base of petiole; postpetiole moderately broadened, 1.1-1.3 times as wide apically as long from spiracle to apex; ventro-lateral carina traceable throughout, strongest on postpetiole; dorso-lateral carina traceable throughout, sharp on postpetiole; dorsal carinae finely detectable on most of petiole and base of postpetiole, strongest apicad; surface of postpetiole smooth and shining with fine, rather weak micro-reticulation which fades out near apex and small, obscure, scattered punctures that emit moderately short, mostly well-separated setae. *2nd gastric tergite:* a little dully shining, with distinct fine and weakly granular micro-reticulation and numerous small, very obscure punctures that emit short, largely widely-separated setae which may become somewhat longer and denser, but not extensively overlapping, laterad and apicad. *Gaster:* rather elongate fusiform; setae of following tergites may be generally somewhat denser than those on 2nd. *Ovipositor:* sheathed portion 0.3 times as long as fore-wing; straight, moderately slender, compressed; nodus low, with a rather large, shallow notch; dorsal valve with a long, nearly direct to slightly concave taper between notch and apex; ventral valve with fine, well-spaced oblique ridges on tip; tip 0.16-0.19 times as high at notch as long from notch to apex.

MALE: differs from female as follows: *Color:* no pale band on flagellum; clypeus more or less broadly white; white on orbits broadly interrupted at top of eye and often not or only slightly interrupted at bottom: band on front-orbit usually broader, particularly on face; that on hind-orbit narrow but with a broader extension across malar space below, or sometimes interrupted on lower ¼ but with a detached mark in malar space; sometimes no white on collar; apex of propleuron sometimes more or less white; white spot on base of tegula; sometimes no white on subalarum; sometimes no white on scutellum or sometimes white spots at base of scutellum even larger than in female; 1st gastric segment mostly black, or becoming more or less pale orange on postpetiole; tergites 2-4 or 5 or 6 pale orange; succeeding tergites blackish, often grading into pale orange laterad and often with dull, narrow whitish apical bands; fore-coxa dully and irregularly to very broadly and brightly white externo-ventrally; fore-trochanter sometimes largely white below; mid-coxa sometimes with a ventral or externo-ventral white spot; mid-trochanter sometimes partly white below; often more or less of hind-tarsomeres 2 (apically) or 3-4 white or hind-tarsus sometimes with only a trace of pale staining. *Length of fore-wing:* 5.7-7.2 mm. *1st flagellomere:* 3.5-4.2 times as long as deep apically. *Malar Space:* 0.9-1.0 times as long as basal width of mandible. *Temple:* 0.8-0.9 times as



Map 1. Distribution of *Trachysphyrus hoplites* n. sp. (Ecuador).

long as eye in dorsal view, a little less strongly receding and often slightly rounded-off. *Mesoscutum:* notauli traceable about 1/2-2/3 the length of mesoscutum. *Wing-Venation:* 2nd abscissa of radius 0.6-1.0 times as long as 1st intercubitus; upper part of nervellus 1.2-2.3 times as long as lower. *Propodeum:* a little longer and lower than in female with basal face more strongly sloping behind; spiracle 1.4-1.6 times as long as wide; basal trans-carina often very sharp and high; apical trans-carina often stronger than in female, but irregular; areola much wider than long in position; lateral longitudinal carinae averaging stronger and less irregular than in female, sharp basally and very high passing onto crista behind. *1st gastric segment:* postpetiole weakly expanded or almost parallel-sided, 0.7-0.8 times as wide apically as long from spiracle to apex; dorso-lateral carina fine but sharp, except sometimes weaker toward base on petiole; dorsal-carinae largely weakly suggested or quite sharp, at least toward apex of petiole and on base of postpetiole; micro-reticulation of postpetiole weaker, fading out well before apex; punctures on postpetiole averaging larger and more numerous than in female, emitting long and often in large part, but not consistently, overlapping setae. *2nd gastric tergite:* punctures obscure, but larger, more numerous, and often more definitely visible than in female, emitting long setae which mostly approach to exceed the length of their interspaces; setae of following tergites a little denser than those on 2nd.

COLLECTIONS: The holotype and five paratypes are in the collection of Henry K. Townes at Ann Arbor, Michigan; a sixth paratype is in the Museum of Comparative Zoology at Harvard University and a seventh in the collection of Charles C. Porter at Metuchen, New Jersey.

DISCUSSION: *Hoplites* differs from all known South American species of *Trachysphyrus* by the following combination of characters: gaster orange in female, black with extensive orange on intermediate tergites in male; clypeal margin unusually sharp and slightly reflexed; subalarum a thin, crescentic lamella; no contrastingly smoother area on mesopleuron along prepectal carina opposite speculum; mediella gently arched; axillus close to hind-margin of wing; propodeal cristae very large and prominently projecting; propodeal spiracle short-oval to almost round; setae of female 2nd gastric tergite for the most part widely separated; ovipositor only 0.3 times as long as fore-wing, its tip only 0.16-0.19 times as high at notch as long from notch to apex.

Within *Trachysphyrus,* the present species is an aberrant member of the cosmopolitan but predominantly Holarctic and temperate South

American *Albitarsis* Group, as defined by Townes (1962, p. 219). Its discovery extends considerably northward the known distribution of the *Albitarsis* Group in Andean South America, for previously no species of this assemblage had been recorded beyond Cuzco in central Perú. There still remains a gap in our knowledge of the *Albitarsis* Group between Ecuador and San José de Costa Rica (Volcán Irazú) in Central America, but the finding of an Ecuadorian species supports the impression that this lacuna is not a natural fact but merely the result of insufficient collecting in the northern Andes.

Among its relatives, *Hoplites* is closest to a species from the mountains of Tucumán Province of northern Argentina[2] with which it shares many features of color, sculpture, wing-venation and proportion but from which it differs principally in its partially orange instead of wholly black male gaster, longer malar space (1.2-1.3 times as long as basal width of mandible in female and 0.9-1.0 times in male versus 1.0 times in female and 0.8-0.9 times in male), very thin instead of rather thick and swollen subalarum, much larger and longer propodeal cristae, and in having a large notch on the ovipositor tip while the Argentine species is almost unique in lacking a notch. The differences noted are of a type which experience has shown to have specific value among the South American *Trachysphyrus*. Nonetheless, we know nothing of what happens to these forms in the mediate Andes of Perú and Bolivia, so that future collecting in those regions might turn up intergrading populations. It seems much more probable, however, that in this case we are dealing with two distinct members of a subgroup which will eventually prove to have several other species in Andean South America.

In addition to *T. hoplites*, only *Trachysphyrus metallicus* (Cameron) is known from the Andes of Ecuador. *Metallicus* is a large, brilliantly blue-green species in which the axillus vein of the hindwing is intermediate between the posterior margin of the wing and the submediella and in which the nodus of the ovipositor tip bears a huge notch that gives rise to a prominent, forward-directed groove. *Metallicus* belongs to the strictly South American *Imperialis* Group and is also the northernmost representative of its series.

Further collecting will probably show that other groups of *Trachysphyrus* are present in Ecuador. The very broad and complex Andean mass which stretches from Ecuador through Perú and Bolivia to northern Argentina appears to be a major center of diversification for *Trachysphyrus* in South America (on the basis of the fairly well collected Peruvian fauna). Indeed, it is likely the first and most important of such centers of diversification as *Trachysphyrus* gives evidence of being an autochthonously Holarctic genus which entered South America from the north along the high temperate corridor afforded by those mountains that buttress the whole western edge of the New World.

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[2] This species is No. 23 in the author's monograph of the South American *Trachysphyrus*. It is not given a name here because there is uncertainty as to whether this shorter paper or the larger work will be published first and it is desired to validate the name of the Argentine species in the latter.

Specific Name: *Hoplites* is a Greek noun meaning "heavy-armed foot-soldier". It was chosen in reference to the tremendous propodeal apophyses that characterize this species.

Acknowledgements: This paper was conceived during a visit to the American Entomological Institute (Ann Arbor, Michigan) made possible by funds from the Evolutionary Biology Committee of the Harvard Biology Department. Dr. H. K. Townes of the American Entomological Institute arranged for the loan of the series described and kindly allowed the retention of paratypes for the Museum of Comparative Zoology and for the author's personal collection.

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STUDIES ON FREE COLONIES OF *CRYPTOCERUS TEXANUS* SANTSCHI (HYMENOPTERA: FORMICIDAE)

By Wm. S. Creighton[1]

For a number of years the writer has hoped to present habit data derived from a study of free colonies of *Cryptocerus texanus*. The need for such a study is apparent if papers previously published in this journal are consulted. Most of the reactions which Dr. R. E. Gregg and I discussed in our 1954 publication (1) were those of captive colonies of *texanus* installed in Janet or Field nests. The limitations of this type of study are shown by the fact that, after more than a year, during which time some of the colonies had been tested with a wide range of food, it was not even suspected that *texanus* subsists on pollen. In 1963 (2) after other inconclusive feeding experiments, the writer abandoned the artificial nests and installed colonies in sealed terraria that permitted limited foraging. The responses of the foragers, which at first seemed to be entirely without point, were finally recognized as activities which resulted in the collection of pollen grains. While their was no reason to suppose that this pollen gathering was an abnormal response, there was good reason to suspect that the process might show interesting new features when carried on by a free colony. Some of these are discussed in this paper. The period during which the free colonies were observed extended from late October to the middle of April.

It may be objected that the term "free colony" as used here is a misnomer. The writer has yet to find an undisturbed nest of *texanus* so situated as to permit easy and continuous observation. The ants are not found in young trees, presumably because these are avoided by the beetles whose abandoned larval burrows are used as nest passages by *texanus*. But an undisturbed nest of *texanus* in a dead limb well up in the crown of a large tree is very nearly inaccessible. And, even if one grants the unlikely possibility that the presence of the colony could be spotted from the ground, there would be no practical way to take advantage of the discovery. Since what was needed for the present study were nests at or below eye-level and since it appears that these are not to be had, a compromise was inevitable. When

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[1] Box 1421, La Feria, Texas.

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limbs containing colonies of *texanus* are pulled down the ants at first show little tendency to leave them. This suggested that if such limbs were wired on another tree at eye-level the ants might remain in them and continue their normal activities with the nest positioned so that these could be easily observed.

The first attempt at this had a discouraging outcome. Two days after a dead oak limb containing a *texanus* colony had been wired to a low limb of a Texas ebony tree, the ants moved out of the oak limb and, taking their brood with them, migrated into the upper part of the crown. Since by doing so they removed themselves from any possibility of further observation, it can only be conjectured that they occupied another burrow well up in the crown of the tree. Much better luck was had with two other colonies when the oak limbs in which they were living were wired, at eye-level to the branches of a grapefruit tree just outside our cottage in La Feria, Texas. This arrangement worked admirably, for although the ants explored many of the burrows in the tree, they remained in the oak limbs during a six months period of observation. Moreover, an examination of the colonies at the end of this time showed that they had done very well for themselves, even though living on a tree that is not ordinarily utilized as a nest site. Since the principal object of this study was to determine whether these colonies behaved differently from captive colonies, two control nests were set up in sealed terraria which were kept inside of the cottage.

It was soon clear that the two groups of nests reacted identically to light and temperature. Foraging, both in the free colonies and the captive colonies, was strictly confined to daylight hours. It would occur only when the temperature was 70°F (21°C) or higher. Because of the greater warmth of the cottage the captive colonies usually began foraging sooner than the free colonies and the latter would not forage at all on cool days. But it was equally clear that the free colonies were often restricted to the nest by another factor for, on very windy days they would not leave the nest, even though the light and temperature conditions were favorable. The foragers from a free nest are much more alert than those in sealed terraria. This alertness makes them hard to observe since they will usually show an avoidance reaction if the observer comes within a foot of them. They will move quickly to the opposite side of a leaf or twig or, when on large branches they may try to hide under bits of loose bark. But there is a much more significant outcome of this alertness for it clearly keeps them from being blown out of the tree. The foragers cling to leaves with the greatest tenacity when these are moved by breezes. The result is, therefore, quite unlike that predicted by the writer in 1963, for the movement of the leaves does not displace the foragers on them. Since I expected that there would be numerous displacements, the ground below the tree was cleared of weeds and smoothed so that any fallen forager would be easily visible. But, although observations were made several times a day over a period of six months, not a single forager was ever seen on the soil at the base of the tree. This statement needs further consideration for the foragers not only managed to avoid being displaced from the tree but they also refused to leave when foraging brought them near the soil. The trunk of the tree in which the nests were placed consisted of a single, large basal trunk about eighteen inches high, which divided into two secondary trunks to form a Y. The crown of the tree was thus divided into two portions and the most certain way to get from one to the other was to travel down one arm of the Y and up the other. This the foragers from the free nests regularly did. But in passing from one arm of the Y to the other the ants were often within a foot of the soil. As they are clearly aware of the presence of an observer at that distance it is inconceivable that they should not have been aware of the soil below them. Yet no forager was ever seen to descend to it. Since *texanus* is not known to nest in grapefruit trees, there is a possibility that this behavior was abnormal. If so it seems odd that the abnormality should have prevented the ants from doing the one thing that might have led them to a more acceptable nest site. In my opinion their behavior was normal and, if this is correct, we now have support for the view that *texanus* forages only in trees and that its presence on the ground may be regarded as the result of an accident. Moreover, there is reason to believe that such accidents are much less frequent than was formerly supposed.

When a free colony of *texanus* is foraging actively it is impossible to keep track of the foragers, since they are scattered all over the crown of the tree. But if the beginning of foraging is observed in the morning it is possible to get some idea of the number of workers engaged in it by counting how many workers leave the nest before any return to it. On this basis the number of foragers was surprisingly small, for it appeared that there were seldom more than twenty outside the nest at the same time. More often there seemed to be no more than a dozen workers engagd in foraging. After a number of counts of this sort the writer came to the conclusion that even the most active of the free colonies must be a small one. It was, therefore, a surprise when this colony was exposed on April 11, to find that it contained twelve queens, fifty-six majors and one hundred and twelve medias and minors. It is hard to explain why so few of the latter leave the nest but this behavior accords well with earlier observations on captive colonies, where the majority of the members spend long hours packed into a nearly immobile mass near the outer end of the nest passage. It is possible that with the higher temperatures which occur during the summer months a greater percentage of the colony engages in foraging. But in this connection it is well to remember that the colony exposed on April 11 contained ten pupae, one hundred and ninety-two larvae and one hundred and seventy-eight eggs. Despite the small number of foragers it is plain enough that their activities had brought through considerable winter brood and this is supported by callows and advanced brood taken from other nests as early as February 11.

It was originally supposed that the free colonies would have to be supplied with food, since the mature grapefruit leaf lacks pollen-trapping hairs. The foragers from the free colonies soon overcame this difficulty by utilizing a transient pollen trap on the young leaves. Each of these has an expanded flange at either side of the petiole and before the leaf reaches full size there are sticky hairs on the lower surface of these flanges. Even though they are evanescent, these hairs supplied the colonies with sufficient pollen to keep them in good condition. The foragers from the free colonies also fed on honey-dew when they could get it. Their reaction here was similar to that described by Creighton and Nutting for *Cryptocerus rohweri* in 1965 (3). The aphids (presumably *A. sphaericola*) had covered the leaf surface with a film of honey-dew and it was this, rather than the aphids which interested the *texanus* workers. The ants appeared to care nothing for the aphids, for they pushed them aside and walked over them in order to get at the honey-dew. The aphids plainly disliked this treatment for they would often withdraw their mouthparts and move to another part of the leaf. It seems well to note that in the Rio Grande Valley aphids are present in significant numbers only during two rather brief periods, one in early spring, the other in the fall. If these same conditions hold over the entire range of *texanus* it is likely that honey-dew plays little part in its diet.

The control colonies had to be provided with food, but this difficulty was unexpectedly simplified when it was found that Tillandsias trap large numbers of pollen grains. There are two species of this epiphyte in the Rio Grande Valley, *T. usneoides* ("Spanish moss") and *T. recurvata* ("ball moss"). Each of these plants has elongate, strap-like leaves which are covered with a reticulum of thin, white, semi-erect scales that largely conceal the green surface beneath them and give to the plants their characteristic grey color. Large numbers of pollen grains are trapped in the spaces between these scales and the ants have no difficulty extracting them. The advantages of using Tillandsias as a pollen source for captive colonies of *texanus* are outstanding. Since the epiphytes will stay fresh indefinitely, an ample supply can be kept on hand without difficulty and, when they are introduced into the terraria, there is no need to provide them with a water source. After a few weeks it became clear that the captive colonies could be kept in excellent condition with no food source other than the pollen grains trapped on the Tillandsia leaves. This was a most surprising discovery for, if captive colonies can subsist on nothing but Tillandsia-trapped pollen, free colonies should be able to do so as well.

The significance of this will be obvious to anyone who has tried to arrive at an explanation for the diversity of the trees in which the nests of *texanus* have been found. The first data on this, published by Dr. M. R. Smith in 1947 (4), appeared to indicate that *texanus* has no preference for a particular kind of a tree as a nest site. Five of the six trees carried in this list belonged to unrelated genera. By 1954 the number of records had risen to twenty-seven and with this increase there appeared the fact that some selective process must be involved in the nesting responses of *texanus*. In this second list seventeen of the records came from live-oaks and this disproportion (63%) was too great to permit the view that any tree is equally suitable as a nest site for *texanus*. At present the disproportion of records from live-oaks has risen to 71% and, in view of the fact that the remaining 29% of the records are spread over six different trees, it follows that the incidence of nests in live-oak trees is at least eight times greater than it is in any other tree. As soon as it was found that pollen grains are the principal food of *texanus* it became clear that the capacity of live-oak leaves to trap wind-blown pollen makes this tree an especially favorable nest site for *texanus*. This advantage is so striking that the difficulty is not to show why *texanus* usually nests in live-oak trees but to explain why it should ever nest anywhere else. There is a strong temptation to treat other records as accidents and sweep them under the rug, which was essentially what the writer did with them in 1963. If this is done one can then fall back upon the often cited but seldom proved explanation of host plant preference.

But the fact remains that *texanus* occasionally nests in other trees than live-oaks and, with an ant whose responses are as rigid as those of *texanus,* it should be possible to account for why it does so. If the choice is made by the nest-founding female, we muse suppose that she is something of a botanical taxonomist, since the list of trees which she has "chosen" includes representatives of five Families[2]. But the whole concept of host plant selection implies a narrow range of choice, seldom extending beyond a few species within a single genus. It should be obvious, therefore, that whatever the selective mechanism may be, it can hardly be a choice on the part of the nest-founding female.

It occurred to the writer that one possible selective device might be a marginal pollen supply in trees where the incidence of *texanus* colonies is low. Efforts to clarify this brought out several disconcerting items. The mature leaves of Texas ebony and mesquite appear to be completely devoid of hairs of any sort which might act as pollen traps. Moreover, in southern Texas, hackberry and mesquite trees usually shed their leaves by the end of December and remain leafless for the next two months. For a species which matures brood all year long and must forage all year long in consequence, a deciduous tree scarcely seems a logical nest site. But it is now clear that we need not look for pollen traps on the leaves of the trees in which *texanus* is nesting if these trees have Tillandsias growing on them. For the Tillandsias will trap enough pollen to supply the needs of the *texanus* colony and this supply will be equally effective whether the tree is evergreen or deciduous. There are thus two pollen sources to be considered and these are not necessarily interdependent. This can produce a survival differential which might be expressed as follows:

NEST SITE	CHANCE FOR SURVIVAL
live-oaks with Tillandsias	optimum
live-oaks without Tillandsias	good
other trees with Tillandsias	fair
other trees without Tillandsias	little or none

On the basis of the above it is not necessary to attribute a capacity for the selection of suitable host plants to the nest-founding female. On the contrary she can be regarded as hampered in her nest-founding responses since she can no longer utilize soil as a place to found her nest. But, except for this limitation, we may suppose that her reactions at the end of a marriage flight are those of most nest-founding females. If her main concern at this time is to put herself into a safe position as rapidly as possible, it is logical to believe that the nest-founding female of *texanus* would accept any cavity in plant tissue whose opening she could occlude. In securing her own safety the female has also provided for the initial development of the colony, since the occlusion that protects her from predators gives equal protection to her developing brood. But, thereafter, there should be a high mortality among these incipient colonies for, unless the female has occupied a cavity in a live-oak or in some other tree on which Tillandsias are growing, there is scant chance that the colony will reach maturity. If this view is correct the selection involved is not the choice by the female of a suitable host plant but the much more commonly encountered phenomenon which eliminates any organism that has placed itself in a position where survival is impossible.

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[2] Colonies of *Cryptocerus texanus* have been found in live-oak and deciduous oaks (Fagaceae), Texas ebony and mesquite (Leguminosae), hackberry (Ulmaceae), prickly ash (Rutaceae) and Mexican persimmon (Ebenaceae).

There are features in the distribution of *texanus* which accord well with the above view. In the past twenty years the number of records for *texanus* has more than doubled and its range has been considerably extended by the addition of records from Mexico. With this additional information it has become clear that in the lower Rio Grande Valley the incidence of *texanus* is far less than it is in other parts of the range. This region of low incidence extends both north and south of the Valley proper and forms a band, about a hundred miles wide, in which it is exceedingly difficult to find colonies of *texanus*. During six winters of collecting in this area the writer has failed to take a single colony. Indeed, the one record of *texanus* from the Rio Grande Valley appears to be the Brownsville record published by M. R. Smith in 1936 (5). The only live-oaks in the lower part of the Valley are a few trees which have been brought in and planted around houses as ornamentals. For this reason alone it might be expected that *texanus* would not find the lower Valley a particularly favorable area in which to nest. But there is no lack of mesquite, Texas ebony or hackberry trees in the lower Valley and it is hard to see why these trees are so seldom utilized if nothing more than their presence is required. But while all three of these trees are widely and uniformly distributed throughout the lower Valley, the great majority of them are free from Tillandsias. The latter are very sporadic in the Valley, most of them being confined to a few isolated pockets near the river. If it is true that this restriction makes most of the trees in the Valley unsuitable as nest sites for *texanus* there is no need to look further for an explanation of its low incidence there.

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BARRIERS TO GENE FLOW IN NATURAL POPULATIONS OF GRASSHOPPERS

I. THE BLACK CANYON OF THE GUNNISON RIVER AND *ARPHIA CONSPERSA*.[1]

By Robert B. Willey and Ruth L. Willey[2]

Introduction.

The oedipodine grasshopper, *Arphia conspersa,* is polymorphic for wing color in Colorado. This feature may prove useful as a marker for tracing historical patterns of gene flow between populations. The metathoracic wings vary from vermillion through salmon-orange to yellow with several intermediate shades which are almost certainly heterozygous in genotype. Although the known populations of the Colorado Front Range are all polychromatic (Gordon Alexander, personal communcation), populations in the Gunnison River Basin on the Western Slope often are monochromatic. For example, those to the south in the foothills of the San Juan Mountains are uniformly yellow as a rule, and those to the north in the Elk and West Elk Mountains are usually salmon-orange. However, near the Gunnison River, which runs west through the center of the basin, there occurs a complex series of populations in various stages of introgression and separation. We wish first to present the case of the Black Canyon of the Gunnison River which presents a striking example of a topographic barrier to gene flow, reminiscent of the cases of the Abert-Kaibab squirrels and other mammals on the north and south rims of the Grand Canyon in Arizona (Allee, *et al.,* 1949, p. 608; Hall and Kelson, 1959).

The Black Canyon. The canyon is located in the west central part of Colorado, about 60 miles southeast of Grand Junction. It is about 50 miles long, 20 miles of which are included in the Black Canyon National Monument. In forming this deep canyon, the Gunnison River has worn its way vertically through about 2000 feet of hard pre-Cambrian rocks, primarily gneiss and granite. The river

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Explanation of Plate 5

Southeastward view of the North and South Rims of the Black Canyon from Fruitland Mesa. Grizzly Gulch (locality #23) is the valley in the foreground, Coffee Pot Hill and Poverty Mesa are in the upper left background.

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has the unusually steep average gradient of 43 feet per mile for the 50 miles length of the canyon. Within the monument boundaries the rate of fall is 95 feet per mile — all without a major falls. The downcutting power of the river is so great that the minor tributaries flowing from the rims generally have not been able to keep pace and are left as hanging tributaries or narrow precipitous gulches. Only a few actually reach the river. The canyon is probably not more than two million years old, representing an average cutting speed of one foot per thousand years.

Several historical accidents contributed to form the Black Canyon (Hansen, 1962): 1) the Gunnison River was already cutting through soft overlying lava flows when the Gunnison Uplift gradually rose for a second time. The river was committed to the channel and was just able to keep cutting through the hard basement material in pace with the rising land. 2) The rock down-stream from the upthrust was much softer, thus maintaining the river's cutting gradient through the canyon. 3) The water catchment capability of the mesas which were formed by the upthrust is meager and most of the streams are dry except for a month during the spring snow melt. Thus side canyon erosion is negligible or directed away from the canyon rims. 4) Fractures and joints in the rock are vertical or, in many places, virtually non-existent. Lateral erosion then results in perpendicular sheering and nearly vertical walls. All of these factors contribute to the formation of a canyon with an average depth equal to or greater than its average width, with cliffs falling sheer 1000-2000 feet to the river below. At the Narrows the depth is 1750 feet, the distance between the rims is 1100 feet, and the width of the canyon at the river is 40 feet, a depth-to-width ratio unmatched by any other major North American canyon.

The mesa formed by this block upthrust and split by the Gunnison River averages 8000 feet in elevation ± 300 feet, whereas the surrounding valleys to the south, west and north average less than 6000 feet. The vegetation on the mesa top is characterized by a chaparral composed of Gambel's oak, service berry, mountain mahogany and isolated stands of Utah juniper and pinyon pine. Grassy openings are scattered through the thick brush and the populations of *Arphia conspersa* reach their greatest density in these open areas. Average rainfall is estimated from records kept at the Monument Headquarters on the South Rim to be about 10 inches per year, at least half of it falling as snow during the winter. For the past three years at Monument Headquarters the prevailing winds at 1:00 P.M. have been south to northwest, with the mode in the west and southwest. However, this varies from year to year with too many variable factors involved to be very meaningful. There is no observable difference in vegetation or climate between the two rims which also are nearly identical in elevation.

To the south, west and north the area is surrounded by arid barren lands ("Dobe Hills") and irrigated farms, areas in which *A. conspersa* has not been found. The primary Gunnison uplift continues to the continental divide on the east, however, with grasslands and forest openings favorable to maintaining large populations of the species.

Arphia conspersa. This species is characteristic of the western Great Plains and foot hills of both slopes of the Rocky Mountains from Northern Mexico to the Canadian plains provinces. In all of its range it is springbrooded with the nymphs overwintering and emerging as adults a few weeks after the snow melts or at the onset of warm weather. Therefore the peak of population activity is altitude and latitude dependent. At the Black Canyon the peak in "typical" years occurs probably in late May at 6000 feet and is delayed until mid-June or later at 8000 feet on the rims of the canyon. The phenology is dependent on the "lateness" or "earliness" of the season as well. The population at 8000 feet reached its peak during the second week of June in 1966 and the last week of June in 1965 — a heavy snow year.

Our studies of this species' behavior are not yet published; therefore a brief summary of its biology is in order. *Arphia conspersa* is a remarkably sedentary species, considering its flight capabilities and its active behavior. Its low vagility (Allee et al, 1949, p. 213) is probably caused in part by complex social interactions which include short spontaneous flights, primarily by the males, only 6 to 10 feet in length. During these flights the wings make a buzzing sound or crepitation. Adult males and females tend to gather in interacting sub-deme groups. The size of each cluster is seldom more than 100 to 200 feet in radius regardless of the extent of the suitable habitat. Seldom does the density of the male population reach 60 per acre even in the clusters; 10 to 20 males per acre in suitable habitat is the usual population. Females are more sedentary and seldom fly except as young adults.

Cloudy, windy weather suppresses flight activity markedly. These insects often become so immobile that they can be picked up by hand — if they can be found. *Arphia* is a relatively small grasshopper and there is little heat storage in its body. Slight meteorological changes register quickly on the activity of the population. At air velocities of about 6 miles per hour at three feet above the ground, we have consistently observed cessation of spontaneous flights and at ten miles per hour cessation of 90% of the escape flights. The insects creep into rock crevices and into clumps of grass, becoming difficult to dislodge. *A. conspersa* is reluctant also to fly more than a few feet over a radically changed substrate such as an asphalt road. A typical maneuver of this insect is to curve back and land at the grassy side, even if it means coming back to the investigator. Stronger fliers, such as *Xanthippus, Cratypedes,* and *Circotettix* show no reluctance to fly over such changes in substrate.

Long escape flights of several hundred feet with the wind will occur in response to strongly disturbing stimuli. These escape flights are silent and can occur at lower temperatures than the normal lower threshold of the spontaneous flights. However, our studies indicate that males seldom move more than two hundred feet and tend to stay within the area of the sub-deme cluster. Long escape flights are rare and usually occur in response to unusual harassment — as by the investigator. On the other hand, spontaneous crepitating flights by the males are frequent during the four-week mating and egg-laying season. As the population ages, however, males show decreasing persistence in courtship and make fewer flights. Whatever dispersion of *A. conspersa* by flight occurs, then, is restricted to a relatively short session in the Spring and may include the very infrequent escape flights of males and young females. Nothing is known about the vagility of nymphs.

The preferred food plants of *A. conspersa* are narrow-leaved grasses such as *Poa palustris;* broad-leaved forbs are not eaten even in captivity unless the insects are starving. Bare spaces between bunches of grass appear necessary for courtship interactions and moist ground nearby tends to lengthen the life span of the population by several weeks. However, the species is seldom found in tall grass meadow, on bare rock slopes, in thick forest or dense chaparral unless there are short-grass openings of at least an acre in area. Irrigated farm land with luxuriant meadows is likely to have *A. conspersa* only along the unirrigated road sides or in low density on rocky knolls which have much of the original grassland intact. Thus, although it is a common and wide-spread species, it tends to have rather restricted habitat preferences and, owing to its social behavior, tends to settle

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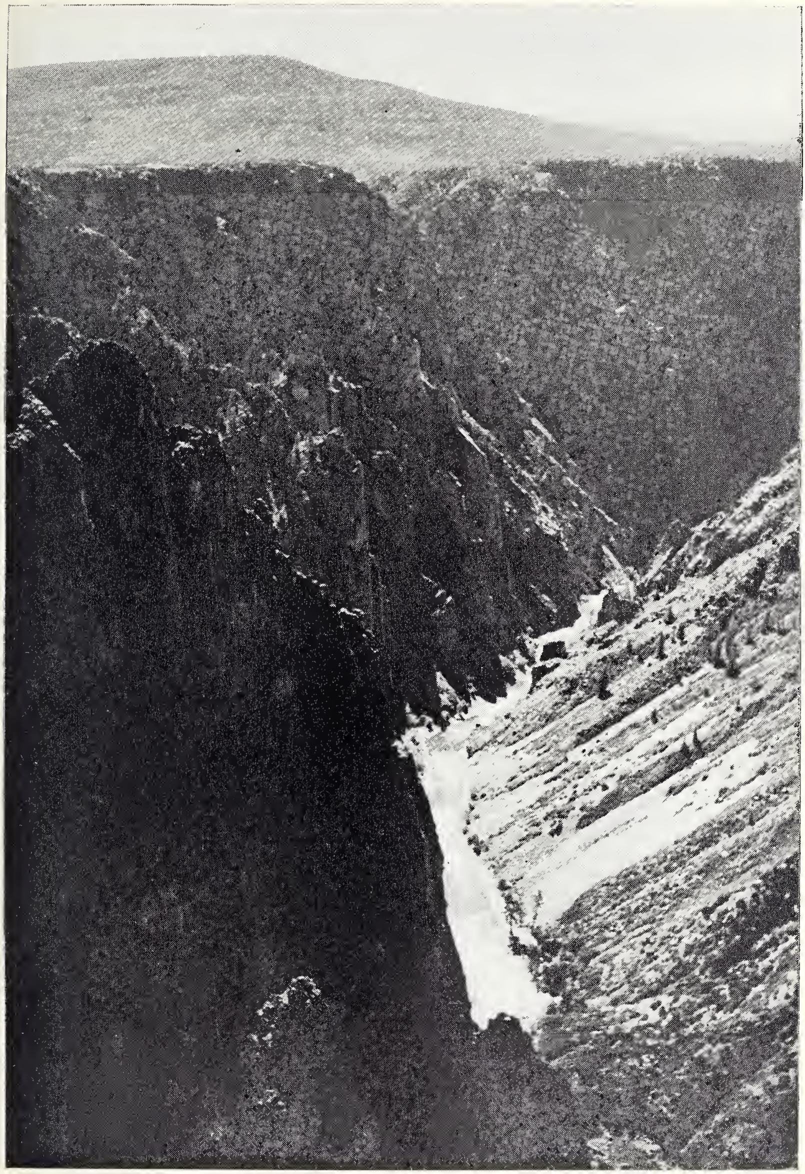
EXPLANATION OF PLATE 6

The Gunnison River within the Black Canyon viewed from Pulpit Rock on the South Rim. The rim walls rise 1700 ft above the river at this point. at this point.



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in small demes and clusters isolated by several sorts of barriers, some of which would seem insignificant to a casual observer. It is fortunate that much of the Gunnison Basin is so far undisturbed by man and allows a base line for analysis of geographic variation in this species.

METHODS

The basic requirement was to make a large enough sample to be reasonably accurate within the limited available time and yet not disturb the composition of the next generation. Therefore capture sampling methods were not used except for special purposes. In each locality we tried to count over 200 individuals on an area of 30 to 50 acres. The sex ratio observed was typically greater than 10 males to one female due to the lubberly behavior of the females. We estimated the average density as 10 to 20 males per acre, so the sampled population was between 20% and 30% of the total male population of the sampled area. Each observer selected a different sector and walked a non-repeating path through likely areas of heavy grasshopper concentration. As the insects made their escape flights or spontaneous social flights, the color of the wings was classed as either orange or yellow, since intermediate shades are difficult to distinguish from orange during flight. The landing place of each individual was noted and if an insect subsequently flew up within a foot of that area it was ignored, unless the color were the opposite shade. If there was any doubt as to whether an insect was an independent observation, it was not counted. Since the average density was about 10-20 per acre and the greatest density was about 60 per acre in isolated clusters, we had no difficulty in tracing individuals.

One difficulty was noted early in the study; often the orange wings would not be visible because of shadow or peculiar angles and the yellow abdomen of the male would flash brightly instead. For this reason, any indefinite yellow-flashing individual would be forced to fly again. A second chance of error in sampling is the probability that the rarer color is counted more accurately than the dominant color. If a counted grasshopper should land near another of the same color and only the second one should fly up again, by our rules it would not be counted, whereas one of a different color would be counted. Therefore, the wing-color variant which is rare in the population could conceivably be of a lower frequency than actually recorded. A third difficulty encountered was the presence of another species of springbrooded oedipodine, *Xanthippus corallipes,* whose wings typically flash lemon-yellow in flight. Pink-winged variants occur rarely in these populations. Experienced observers can easily distinguish the two species in flight by shade differences, banding of the wing, and flight behavior. Here again, any individuals which could not be checked with certainty were not counted. All the observers were experienced enough to be accurate by the time they started work on these localities. Later in the season, several other bandwing species begin to appear, but they are all easily distinguished in flight from *A. conspersa.*

The most productive time for counting the population was between 10 AM and 4 PM on clear warm days. Since the peak for each population lasts only two weeks, and three or four observers take an average of 1½ hours to count a sample of 200, time is an important factor.

A second method was to collect about 50 specimens as nearly at random as possible. This usually took longer than merely counting 200 in the field and required additional curatorial time. However, we did collect from large populations and in this way we could check on the frequency of various shades of presumed heterozygotes. Recently, laboratory breeding of individuals from selected localities has proved successful, and the genetic analysis when completed will be reported later.

RESULTS AND DISCUSSION.

The accompanying maps and table (figs. 1 and 2, and plate 7) show the wing-color proportions of each sampled locality between Sapinero and Green Mountain Reservoir. The most striking difference between the populations of the North and South Rims occurs within the National Monument itself. In more than three years of intensive sampling, populations of the monument's North Rim have never been observed to produce a yellow-winged individual ($n=1355$), whereas the South Rim's population varies in a cline from $<65\%$ yellow in the west to $>90\%$ yellow at the eastern boundary.

First we shall consider the physical properties of the canyon rims. On both the South Rim and North Rim the grass habitat is quite discontinuous. Grassy openings in the chaparral are often separated by several hundred yards of dense brush. In this way, the rim populations are broken up into semi-isolated units which show sharp clinal variation which is less dependent on distance than on the density and impenetrable nature of the chaparral barrier. For example, the populations on the South Rim (fig. 1) along the relatively continuous grassy areas locality from Sunset View (#3) to Gunnison Point (#6), a surface distance of three miles, are stabilized at 33% to 36% orange. At the campground (#7) the proportions vary from

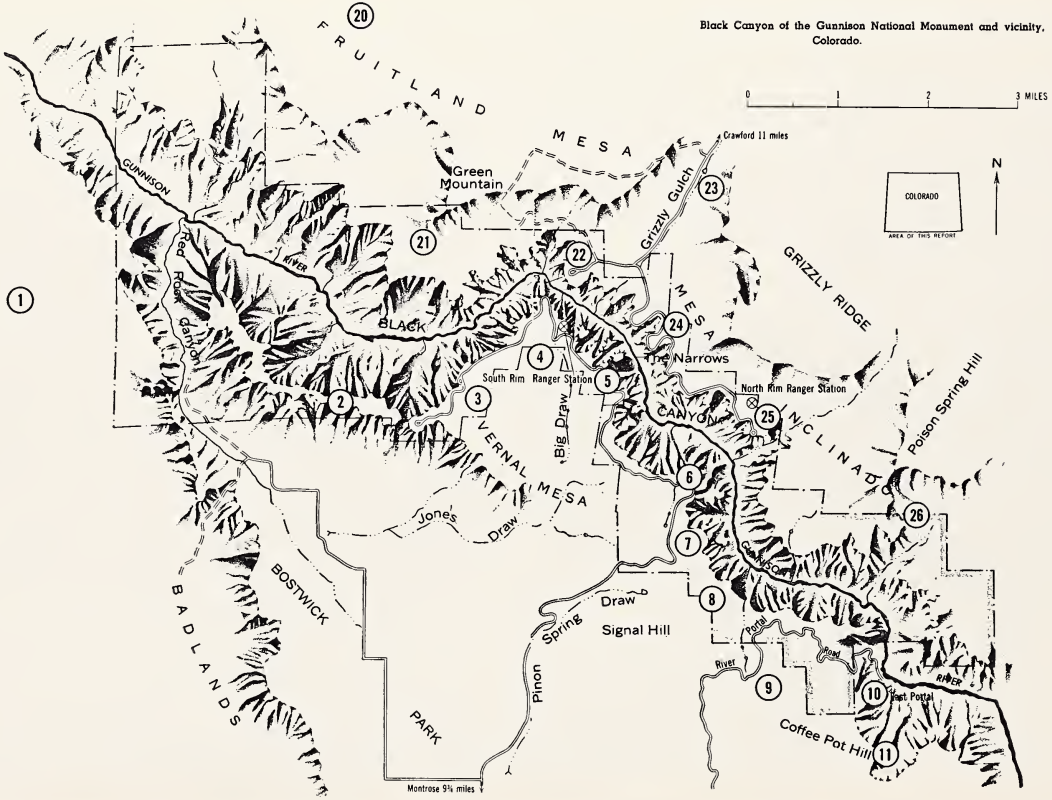


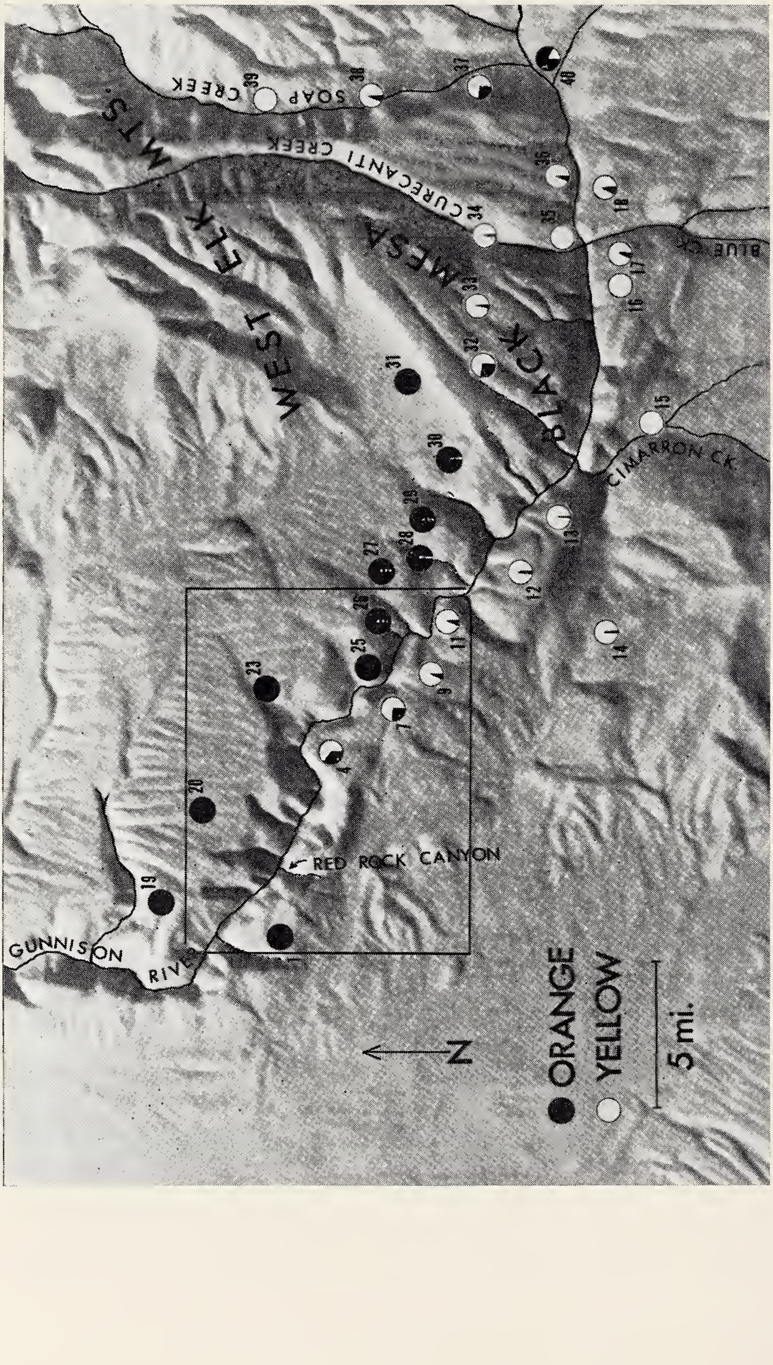
Fig. 1. Black Canyon of the Gunnison National Monument and vicinity, Colorado. Map modified from Hansen, 1965.

21 to 29%. Then in a distance of only 1½ miles across dense chaparral the proportions drop to 6% orange (n=187) at the head of East Portal Canyon (#9). Late in the season of 1966, we sampled the area between these two localities and found only three openings in the chaparral ranging from about 5 to 10 acres each. The proportions were about 10% orange in each habitat (total n=87, locality #8). Recently, trails six feet wide through the brush have been cleared to allow cattle access to the grass. Several *Arphia* were found on these trails between the meadows. Chaparral in this area is 6 to 8 ft tall and impenetrable to man. It is clearly a major factor in the isolation of *A. conspersa* demes.

Continuing eastward along the South Rim (plate 7), the proportions of orange diminish gradually to zero on Fitzpatrick Mesa (#16). Then on the eastern portion of the mesa (#17), orange individuals appear in small numbers. The proportions rapidly increase eastward to Sapinero (#40), where the Black Canyon begins. This population was about 85% orange and showed the influence of a major orange-winged population continuous with the Elk Mountain centers north of the river. The presence of a large isolated yellow population in the Soap Creek Valley *north* of Sapinero and the Gunnison River illustrates the complexity of the geographic variation in the eastern populations. On Black Mesa a line of aspen-spruce forest 2 miles wide separates the eastern yellow outpost (locality #32, 28% orange, n=126) from the north-western orange-winged populations (at #31, 100% orange, n=108) as effectively as the Black Canyon does.

Westward along the North Rim of the canyon, the orange populations afford less obvious clinal variation than is true with the South Rim populations. The eastern demes near the zone of contact with the Soap Creek yellow, though counted by sight transect as all orange or with less than 1% yellow, include some lighter orange individuals — presumably heterozygotes. Collections show a complex phenotype series which so far has defied biometric analysis. Genetic analysis of each phenotype is now underway in laboratory matings.

Turning to the canyon itself, only three areas seem to have suitable and continuous habitat down to the river on both sides to afford a crossing point. These points are, west to east, Red Rock Canyon and an unnamed canyon (#1) just west of it, East Portal (#10), and Blue Creek. West of Red Rock Canyon the southern population is uniformly orange (n=86) and may be the source of the orange



Willey and Willey — Barriers to Gene Flow

variants of the eastern South Rim demes. Red Rock Canyon[6] has so far been inaccessible to us at the proper season. The East Portal deme[6] at the river's edge has its peak too early in June for researchers with academic responsibilities, but a count of the last survivors on the south side of the river in mid-June, 1966, showed 10 yellow and 2 orange, whereas a deme at the head of Spring Gulch (#28) across the river and one mile north-east was >99% orange (n=262) and less than a mile south of the river at the head of East Portal Canyon (#9) the population was 94% yellow (n=187). The river-edge populations at the confluence of Blue Creek and Curecanti Creek are inaccessible so far because of the seasonal factor and the construction of Morrow Point hydroelectric dam. However, the map (fig. 4) indicates that here, too, is a probable crossing point because of the similarity of population proportions. There is continuity of marginal habitat, also. Undoubtedly there is a strong influx of genes for yellow wing color from Soap Creek Valley, as well.

At all other points we have found gulches, such as Dead Horse Gulch (#26) on the North Rim, which reach the river with fairly continuous habitat, but the opposite wall rises as a jumble of bare rocks and precipitous cliffs, creating an effective barrier to further movement. The banks of the river are either overgrown with brush, blocked with talus or composed of gravel bars with no grassy openings larger than a few square yards. High water marks 5 ft above the June water level indicate early spring flooding of the banks with accompanying great turbulence, making it unlikely that overwintering nymphs could survive on the infrequent sandy shores of the river.

In addition to the effect of distance and difficult terrain, the effect

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[6] We were able to study the early populations during May and June of 1967. Results pertinent to this report are as follows:

a. Head of Red Rock Canyon, 6700-6780 ft., 100% orange-red (n=109), May 8 (May 9 transect of canyon to Gunnison River yielded 100% orange, n=25).

b. East Portal at Gunnison River (locality #10) 47% orange (n=58), May 7.

c. Pioneer Lookout (locality #35), 100% yellow (n=128), June 5.

The unexpectedly equal proportions of orange and yellow at East Portal indicate downward gene flow from both rims along the side canyons near this point with significantly less upward flow. It is doubtful that there is an important additional pathway along the river, due to the apparently great discontinuities of suitable habitat.

EXPLANATION OF PLATE 7

The Black Canyon Area. The section within the marked rectangle is shown in greater detail in Fig. 1. Numbers correspond to the locality numbers in the table, Fig. 2. Ideas on format thanks to Wallace Hansen.

of altitude on the phenology of populations within the canyon is of interest. For example, at the head of East Portal Canyon and nearby Coffee Pot Hill (elevation 8600 ft), on June 15, 1966, the insects were at their reproductive peak with high population density, numerous pairs *in copula* and constant spontaneous flights. Within the canyon at East Portal (elevation 6500 to 6700 ft) on June 19, 1966, the population was nearly non-existent. The males which were observed seldom flew and several which were captured had worn wings and missing legs. The climatological conditions were essentially identical and were optimal for behavioral interaction. On July 21, 1965, the previous year, the population at the head of East Portal Canyon was clearly senescent, whereas no Arphia could be found below at East Portal. Indeed *Trimerotropis sparsa,* a summer-brooded oedipodine, was at its peak.

CONCLUSIONS

It is doubtful that significant gene flow in *Arphia conspersa* occurs across the Black Canyon except at the three isolated points mentioned and these may be quite minimal. If it did, we would have to explain why the North Rim population is so free of the yellow phenotype and the eastern South Rim is so nearly free of the orange phenotype. We should expect the recorded SW winds to carry a winged species across the relatively short aerial distance between the two rims with a resulting admixture of the yellow phenotype in the now completely orange-winged populations of the North Rim. But examination of the data shows that this has not happened to any significant degree. Besides, the behavior of this species is not conducive to transport by wind, since increased velocity of wind suppresses flight activity. As we have seen, persistent chasing can force an *Arphia* across the road or over a hedge or down a gulch, but such pursuit is an artificial situation which seldom occurs in nature. Nearly constant canyon updrafts definitely prevent flying out over the cliff edges and flocks of swallows are active during the day at the rim edge, affording another efficient barrier to transcanyon gene flow.

There is no obvious indication that habitats of the two rims differ.

Fig. 2. (opposite page). Protocol of *Arphia conspersa* populations and locality elevations.

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[3] Elevations are estimated from the following 7 1/2 minute U.S. Geologic Survey topographic maps: Black Ridge, Red Rock Canyon, Mt. Gunnison, Cathedral Peak, Curecanti Needle, Grizzly Ridge, X Lazy F Ranch, Sapinero, and Little Soap Park.

[4] This is the true Blue Mesa Summit *east* of Blue Creek on U.S. Highway 50.

[5] Several dilute orange and pink-winged specimens were observed or captured, although no yellow-winged individuals were recorded.

Locality	Elevation[3] in Feet	Sample Size	(n)= No. Orange	% Orange (%)=Sample below 100	Sampling Date
1. West of Red Rock Canyon	6450	11		(100)	17-VI-66
	6250	14		(100)	17-VI-66
	6400	62		(100)	17-VI-66
2. Warner Point	8100-8300	11	(8)	(73)	19-VI-66
3. Sunset View	8200	172	(60)	35	19-VI-66
4. Monument Headquarters	7950	223	(75)	34	16-VI-66
5. Devils Look Out to Cross Fissures View	7900	160	(57)	36	28-VI-65
6. Gunnison Point	8200	91	(20)	(22)	28-VI-65
7. Campground — South Rim	8300-8400	209	(43)	21	28-VI-64
		184	(54)	29	23-VI-65
		199	(47)	24	21-VII-65
		296	(66)	22	14-VI-66
		65	(18)	(28)	30-VI-66
8. Between Campground and E. Portal Canyon	8400	83	(7)	(8)	30-VI-66
9. Head of East Portal Canyon	8600	59	(1)	(2)	21-VII-65
		187	(12)	6	15-VI-66
10. East Portal at River	6500-7000	12	(2)	(17)	19-VI-66
11. Coffee Pot Hill	8750	315	(24)	8	25-VI-66
12. Poverty Mesa	9500	131	(5)	4	25-VI-66
13. Sheep's Knob	9400	225	(1)	<1	27-VI-66
14. Cerro Summit	7900	89	(3)	(3)	23-VI-64
15. Rt. 50 — School house Dist. #9	7100	67	(0)	(0)	8-VII-65
16. W. Fitzpatrick Mesa	9100	123	(0)	0	2-VII-66
17. E. Fitzpatrick Mesa	8400	49	(3)	(6)	2-VII-66
18. Blue Mesa Summit[4]	8200	159	(14)	9	27-VI-65
19. Green Mt. Reservoir	7900	12	(12)	(100)	28-VI-66
20. E. Green Mt.	8200	23	(23)	(100)	25-VI-66
21. Serpent Pt. Meadow	8000	46	(46)	(100)	23-VI-66
22. North Rim Campground	7800	48	(48)	(100)	25-VI-64
23. Grizzly Gulch	7700	41	(41)	(100)	25-VI-64
		91	(91)	(100)	30-VI-65
24. Narrows Overlook	7900	88	(88)	(100)	30-VI-65
25. Rangers Station — N. Rim	8000	371	(371)	100	30-VI-65
		288	(288)	100	22-VI-65
26. Dead Horse Gulch	8250	188	(188)[5]	100	23-24-VI-66
27. Dead Horse Mesa	8500	209	(209)[5]	100	25-VI-66
28. Spring Gulch	7800	108	(108)[5]	100	7-VII-65
		262	(261)	>99	26-VI-66
29. Pine Ridge	8200-8400	125	(125)[5]	100	27-VI-66
30. Buckhorn Gulch at Rt. 92	8200-8400	142	(138)	97	7-VII-65
		101	(99)	98	27-VI-66
31. Old Black Mesa Road NFS boundary North	8300	108	(91)	84	25-VI-64
32. Mesa Creek Black Mesa Road Jct.	9600	126	(35)	28	29-VI-64
33. Myers Gulch Road	9400	107	(4)	4	29-VI-64
34. Curecanti Ck at Rt. 92	8000	58	(1)	(2)	28-VI-64
35. Pioneer Lookout	8000	6	(0)	(0)	7-VII-64
		18	(0)	(0)	1-VII-66
36. Haypress Gulch	8000	71	(4)	(6)	28-VI-64
37. Sapinero Guard Stn.	7800	231	(63)	27	27-VI-65
38. Soap Ck. Campground	7700	79	(3)	(4)	6-VII-64
39. Little Soap Park	8000	166	(0)	0	6-VII-64
40. Sapinero at Rt. 50	7600	139	(118)	85	27-VI-65

They are equivalent in elevation, climate and biotic community structure, and are separated by no more than one mile of horizontal space. Nor does the wing-color of *A. conspersa* appear to be influenced by external factors such as humidity, extremes of temperature, etc. Since homogeneous populations of both colors are found in equivalent habitat and climatic extremes elsewhere, ontogenetic and selective hypotheses seem unlikely, although untested experimentally. The wings are kept folded during courtship and the female has no opportunity to see the color of the male's wings; therefore, sexual selection is not likely during the ground interaction, at least. There is, of course, the possibility that color is accompanied by some other trait for wing color pleiotropically determined genetically with some behavioral effects which could have sexual selective value.

As hypothesis alternative to one which assumes selective differences in the two areas supposes that these populations represent partially arrested introgression of two formerly distinct geographic variants which reached the Black Canyon after it had acquired much its present form. It is not yet clear to us what might have caused the homogeneity and isolation of the variant populations — if a polymorphic species was indeed the progenitor. However, our mapping of the populations throughout the Gunnison Basin has shown a large orange-winged population centered near Grand Mesa and the Elk Mountains and a homogeneous yellow-winged population centered in the San Juan Mountains. The analysis of the zoogeography of this species in the Gunnison Basin soon will be completed. Perhaps the heavy Pleistocene glaciation of the area (Richmond, 1965) may hold a clue to the origin of these populations, but such slow speed of gene flow since then may well be due to the slow rate of dispersal — the low vagility of the species due to the combination of social attraction and relatively restricted habitat preference.

Whatever the origin of the homogeneous populations, the barrier of the Black Canyon of the Guninson River evidently acts as a fine-meshed filter with discontinuous habitats scattered infrequently over a spectacularly difficult terrain. The "insularized" populations may also reach their reproductive peaks at different times due to the seasonal effect of altitude on their phenology. Barring undetected selection factors such as predator preference for the rare variant, a filter effect could work multidimensionally to prevent thorough introgression of these two variants.

SUMMARY

The Black Canyon of the Gunnison River in Colorado may be a nearly complete barrier to direct gene flow between populations of the oedipodine grasshopper, *Arphia conspersa.* In this species, a con-

venient marker (wing color) is available which may have been segregated in the source populations elsewhere in the Gunnison Basin during the Pleistocene. The evidence is circumstantial that the northern orange and southern yellow populations reached the Black Canyon area after the canyon had acquired its present form. The clinal variation between demes of the South Rim may be due to southward gene flow of orange-wing across the river at the western end of the canyon and slow lateral movement along the rim. The slow speed of gene flow seems to be due to the sedentary behavior of the adults, spatial discontinuities in suitable habitat and seasonal differences between the rims and the river 2000 ft. below.

ACKNOWLEDGEMENTS.

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STUDIES ON NORTH AMERICAN CARBONIFEROUS INSECTS. 5. PALAEODICTYOPTERA AND MEGASECOPTERA FROM ILLINOIS AND TENNESSEE, WITH A DISCUSSION OF THE ORDER SYPHAROPTEROIDEA.*

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The insects treated in this paper are from the Upper Carboniferous deposits of the "Mazon Creek" region of Illinois and of a new locality in Anderson County, Tennessee. All represent undescribed species, with one exception — the type specimen of *Sypharoptera pneuma* Handlirsch, for which the author erected a separate order, Sypharopteroidea.

I am indebted to Dr. Sergius Mamay of the U. S. Geological Survey and to Mr. Robert Rapp for the opportunity of studying the Tennessee fossil; and to the authorities of the Peabody Museum at Yale University for the loan of the type of the *Sypharoptera*. To Mr. Walter Dabasinskas of Cicero, Illinois, I am especially grateful for his kindness in sending me for study more of the remarkable insects which he has collected in the ironstone nodules near Braidwood, Illinois. The efforts which he and Mrs. Dabasinskas have put into the collecting of fossils in the nodules are a major contribution to the study of Carboniferous insects.

Order Palaeodictyoptera

Family Breyeriidae Handlirsch

This family includes species of large size, having an unbranched MA and CuA, a forked CuP, MP with at least three branches and Rs with at least four branches; cross veins are numerous and somewhat irregular but do not form a reticulation. The hind wings are broader basally than the fore wings but the venation is essentially the same except for the more numerous anal veins.

The family has been found in Upper Carboniferous strata in England, Belgium, France and Czechoslovakia.[1] The species described below is the first from a North American deposit. The generic

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classification of the Breyeriidae has been reviewed by Kukalová (1959); there now seem to be only two valid genera, *Breyeria* Borre and *Strobbsia* Handlirsch. The latter is known from the Upper Carboniferous of England but *Breyeria* is represented in the other European deposits mentioned under the family and is the genus to which the North American species belongs.

Genus *Breyeria* Borre

Breyeria Borre, C. R. Soc. Ent. Belg., 1875: 7; synonyms: *Borrea* Brongniart, 1893; *Megaptiloides* Handlirsch, 1906; *Pseudoborrea* Handlirsch, 1919; *Breyeriopsis* Laurentiaux, 1949.

Breyeria rappi, new species

Plate 8; text-figure 1

Fore wing: length 81 mm.; width 25 mm. Costal margin smoothly curved; costal space with a short longitudinal vein basally; costal space not broadened basally; Sc terminating on R1 just beyond the first fork of Rs; R1 extending to the very apex of the wing; R arising at the level of the fork of M, with six terminal branches; MP with three terminal branches; cross veins mostly straight, a very few branched in the area between Rs and MA; small circular, cuticular thickenings occur between some of the branches of Rs, between Rs and MA, and between MA and MP.

Holotype: No. 158550, U.S.N.M., Washington, D.C.; collected by Mr. Robert Rapp in the "Pewee" Coal Seam at a strip mine near Peach Tree Gap, Anderson Country, Tennessee. The specimen (Plate 8) consists of a virtually complete wing, lacking only a few millimeters of the apex, and it is perfectly preserved. The species is named for Mr. Rapp. Dr. Mamay has informed me (*pers. com.*) that, on the basis of the fossil plants which Mr. Rapp collected in the Pewee Coal Seam, he considers the deposit to be of Lower or Middle Allegheny age. This would correspond closely to the Westphalian C Stage of the European Upper Carboniferous.

This species differs from others in *Breyeria* by a series of minor (but presumably specific) characters, such as the general shape of the wing, the number and arrangement of branches of Rs and the pattern of cross veins. The fossil shows no sign of color markings,

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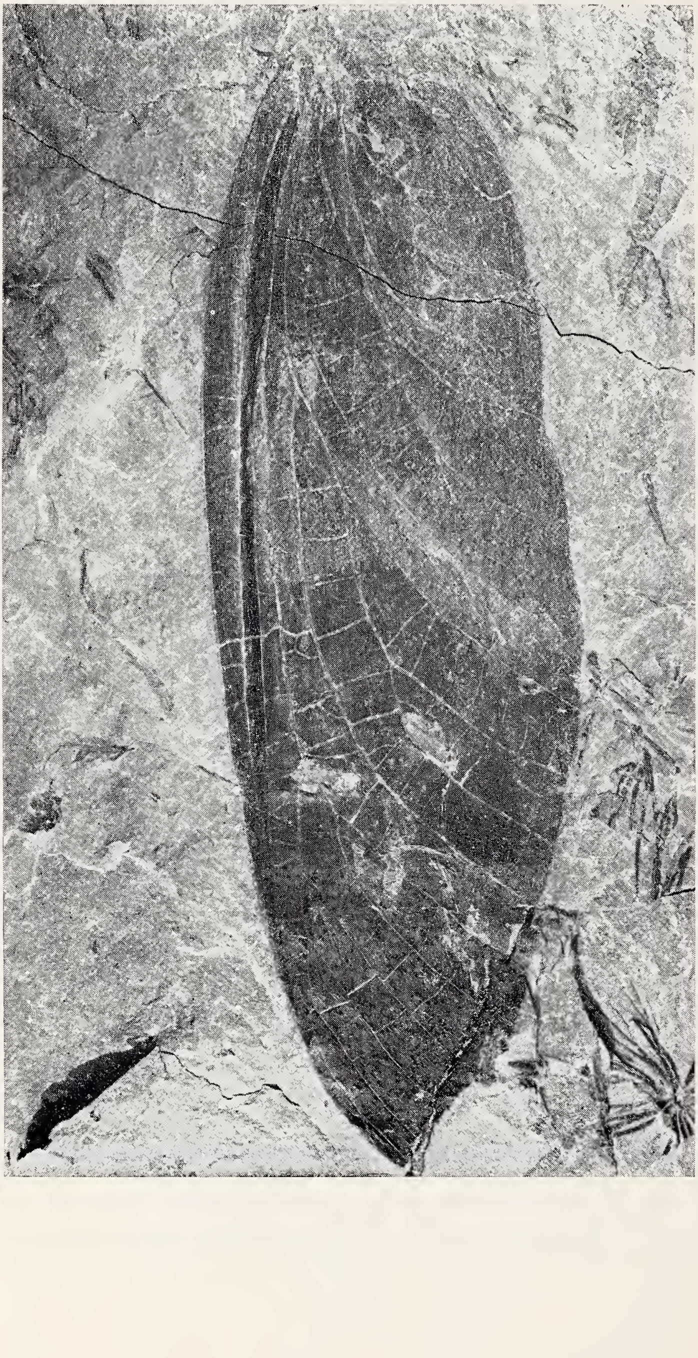
[1] The fossil which Keller (1935) described as *Breyeria constantini* from the Upper Carboniferous of the Ruhr Valley in Germany is so fragmentary that its assignment to any family is problematical.



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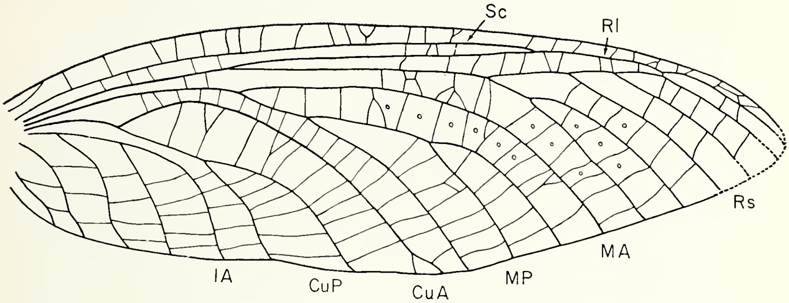
as had been noted by Laurentiaux-Vieira and Laurentiaux (1964) in *Breyeria vrankeni* from the Upper Carboniferous of Holland.[2] It is most interesting and unexpected to find a representative of the family Breyeriidae in the Upper Carboniferous strata of the New World, especially since the fossil shows no differences which separate it generically from the European species. Indeed, the uniformity of the venational pattern of the known Breyeriidae is very striking.



Text-fig. 1. Wing of *Breyeria rappi,* n. sp. (holotype)

The excellence of the preservation of the type of *B. rappi* reveals some noteworthy features. One of these is the presence of a distinct but short longitudinal vein at the base of the costal space. This is undoubtedly comparable to the several ridges of veins that Kukalová (1960) and Carpenter (1964) have noted in other Palaeodictyoptera. It is by no means certain, however, that this vein is the costa or that a true pre-costal space exists, like that in the Protodonata. Laurentiaux has noted (1964) that he finds no sign of this basal vein in the costal area of the species which he studied.

Another interesting feature of the wing of *B. rappi* is the presence of the small, circular, cuticular thickenings between several of the veins. These have been previously reported in the Breyeriidae by Laurentiaux-Vieira and Laurentiaux (1963, 1964). Similar plate-like thickenings have been noted in some of the Protodonata (Bolton, 1914, Carpenter 1947) and somewhat larger plate-like thickenings

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[2] The difference in color between the basal and distal parts of the wing of *B. rappi,* as shown in the photograph, is almost certainly due to peculiarities of preservation rather than to pigmentation in the wing of the living insect.

EXPLANATION OF PLATE 8

Breyeria rappi, n. sp. Photograph of holotype. Upper Carboniferous of Tennessee. Length of wing, 81 mm.

occur in the Diaphanopterodea (Carpenter, 1963) and in some of the orthopteroids. There is no basis, however, for regarding these as nygmata, a term which was used by Navas for certain clear, cuticular spots on the wings of some Trichoptera, Neuroptera and related Endopterygota (see Carpenter, 1963, p. 243, footnote).

Family Fouqueidae Handlirsch, 1906

This family has previously been known only from the Upper Carboniferous shales of Commentry, France, in which it is represented by the genus *Fouquea* Brongniart and four species. The characteristics which seem to be peculiar to the family are the combination of a branched CuA and very numerous cross veins, which form a true reticulation only along the posterior portion of the wing. The branched CuA, which is not found in the more primitive Palaeodictyoptera, is a characteristic of the Spilapteridae also, but the cross veins in that family are very few in number and are usually aligned to form gradate series.

Mr. Walter Dabasinskas of Cicero, Illinois, has recently sent me a specimen of a palaeodictyopteron which has the same combination of characteristics given above for the Fouqueidae. It cannot, however, be referred to the genus *Fouquea* and is therefore taken as the basis of the new genus described below.

Genus **Neofouquea,** new genus

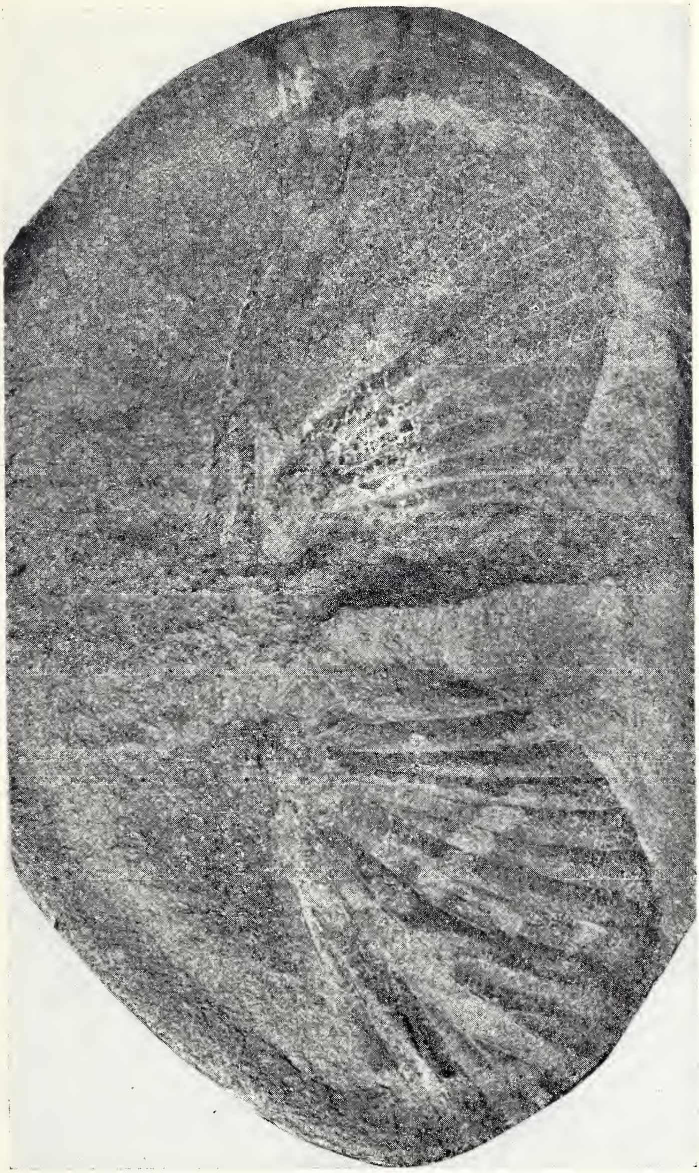
Subcosta closer to R and R1 than in *Fouquea*; CuA deeply forked, i.e., to about the same level as the fork of M into MA and MP; CuA dichotomously branched; CuP deeply forked, without additional branches. Wings with two slightly curved rows of maculations in the basal half; additional maculations probably present in the more distal part of the wing.

Type-species: *Neofouquea suzanneae,* n. sp.

In contrast to this genus, *Fouquea* has a pectinately branched CuA and a multiple branched CuP, CuP1 having three or four terminal branches. The cross veins in *Neofouquea* seem as close together as they are in the other known species of the family Fouqueidae.

Explanation of Plate 9

Neofouquea suzanneae, n. sp. Photograph of holotype. Upper Carbonirerous of Illinois.



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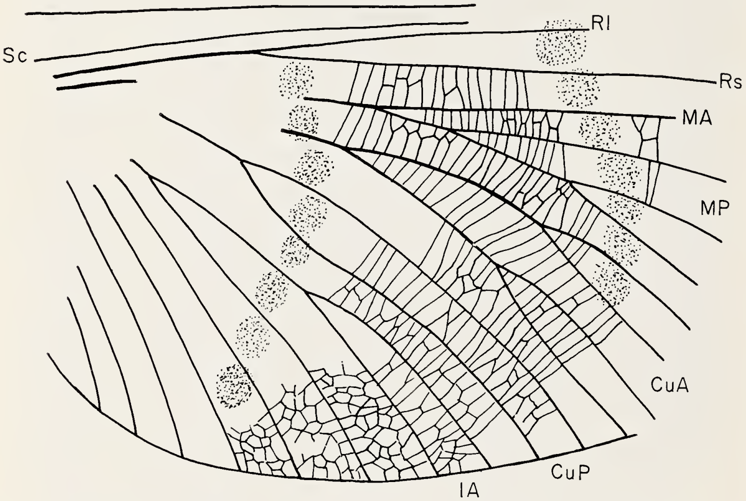
Neofouquea suzanneae, new species

Plate 9; text-figure 2

Length of wing as preserved, 30 mm., maximum width, 22 mm.; estimated length of entire wing, based on comparison with species of *Fouquea,* 65-70 mm. Since only the basal half of the wing, is preserved, the forking of Rs and of MA is unknown, but both of these veins arise much as in the species of *Fouquea*; MP forks shortly after its origin, MP1 being without a branch in the preserved portion of the wing, but MP2 is dichotomously forked at about the level of the outer row of maculations; CuA divides at about the level of the first division of M, much as in *Fouquea*; CuA1 and CuA2 are forked to about the same level; CuP is deeply forked, producing a nearly straight CuP1 and a somewhat sigmoidally curved CuP2, as in the other Fouqueidae; the two branches of CuP are close together, without secondary branches; the first two anal veins arise from a single stem and the anterior one is forked but not so deeply as in Fouquea. Several anal veins appear to radiate from a basal stem, although their proximal portions are not preserved. The cross veins form an irregular reticulation in the distal portions of the anal veins and along the posterior border of the wing near CuP; in other regions the cross veins are nearly parallel, very close together and only infrequently have connecting branches. An inner



Text-fig. 2. Wing of *Neofouquea suzanneae,* n. sp. (holotype).

row of maculations, consisting of irregularly circular spots, occurs at about the level of the origin of Rs and just beyond the fork of CuP; the more distal row occurs just beyond the level of the fork of MP2 and CuA1; there are apparently eight spots in each of the rows.

The type specimen, which is in the collection of Mr. Dabasinskas, Cicero, Illinois, consists of basal portions of two wings (see Plate 9). The main veins and the cross veins are well preserved and the maculations are clear. The species is named for Suzanne Dabasinskas, in recognition of the persistence and patience which she, as well as her husband, Walter Dabasinskas, have shown in their collecting of the Mazon Creek insects. The specimen of *N. suzanneae* was collected between Braidwood and Coal City Illinois (Will Co.).

Since no satisfactory figure of *Fouquea lacroixi* Brongniart (the type species of the genus) has previously been published, I include here a drawing of the venational pattern of the type based upon study of the fossil at the Institut de Paléontologie in Paris. A comparison of the venation of *lacroixi* with that of *suzanneae* indicates that the type specimen of the latter consists of the basal half of the wing, not quite as far distally as the first branch of the radial sector or of the fork ofMA. The greater width of the wing of the specimen of *suzanneae* and the curvature of CuA suggest that the specimen is part of a hind wing, not a fore wing; however, since no complete specimen of the family Fouqueidae has been found, we do not have certain knowledge of the difference between the front and the hind wings.

The densely arranged cross veins, which are clearly indicated in the type of *suzanneae*, are similar to those of the several species of *Fouquea* in the Commentry shales. They are present in the type of *lacroixi*, although they were not represented in Brongniart's figure of the fossil. They are, however, especially clear over the entire wing of the type of *F. superba* (Meunier), as shown in the accompanying photograph (Plate 10).[3]

The specimen of *Fouquea lacroixi* shows prominent maculations on the wings, arranged in irregular rows, as depicted in Brongniart's figure (1893, plate 19, fig. 10). Specimens of the other species of *Fouquea* [i.e., *comstocki* Lameere, *needhami* Lameere, *superba* (Meu-

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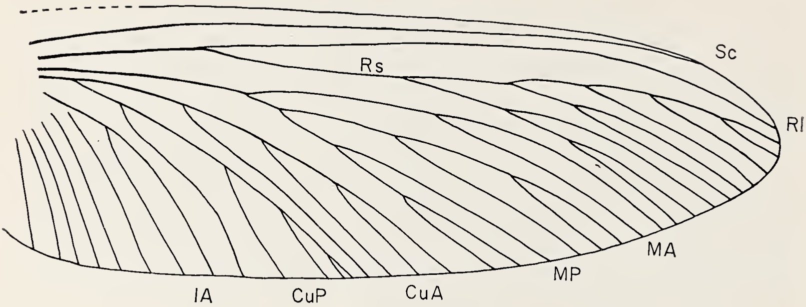
[3] The genus *Archaecompsoneura*, which was established for *superba* (Meunier, 1909), is a synonym of *Fouquea*, as noted by Lameere (1917), although this is not apparent from Meunier's grossly inaccurate figures (1910, 1912).



Text-fig. 3. Wing of *Fouquea lacroixi* Brongniart; original drawing based on type specimen in Institut de Paléontologie, Paris. Upper Carboniferous of Commentry, France.

nier)] show similar patterns. The maculations on the wings of *suzannaea* are much smaller and are arranged in definite rows, as shown in the photograph, Plate 9.

The only palaeodictyopteron described from the ironstone nodules of Illinois that resembles *N. suzanneae* is *Diexodes debilis* Handlirsch (1911), which was based on a small, poorly preserved wing fragment. However, the cross veins in *debilis* (the type of which I have examined at the Peabody Museum) are relatively few in number and do not, therefore, form the dense pattern characteristic of the Fouqueidae.

Order Megasecoptera

Family Brodiidae Handlirsch, 1906

This family was established by Handlirsch for a single species, *Brodia priscotincta* Scudder from Upper Carboniferous deposits in England. From the time of its description in 1881, this species has presented numerous problems with respect to both the nature of the structures preserved and their phylogenetic interpretation. Although numerous specimens (at least 15) have been subsequently found, these have consisted only of isolated wings or fragments of wings; nothing is known, therefore, of the differences between the fore and hind wings or of the body structure. The relationships of *Brodia* have been uncertain. Handlirsch placed the family at first in the

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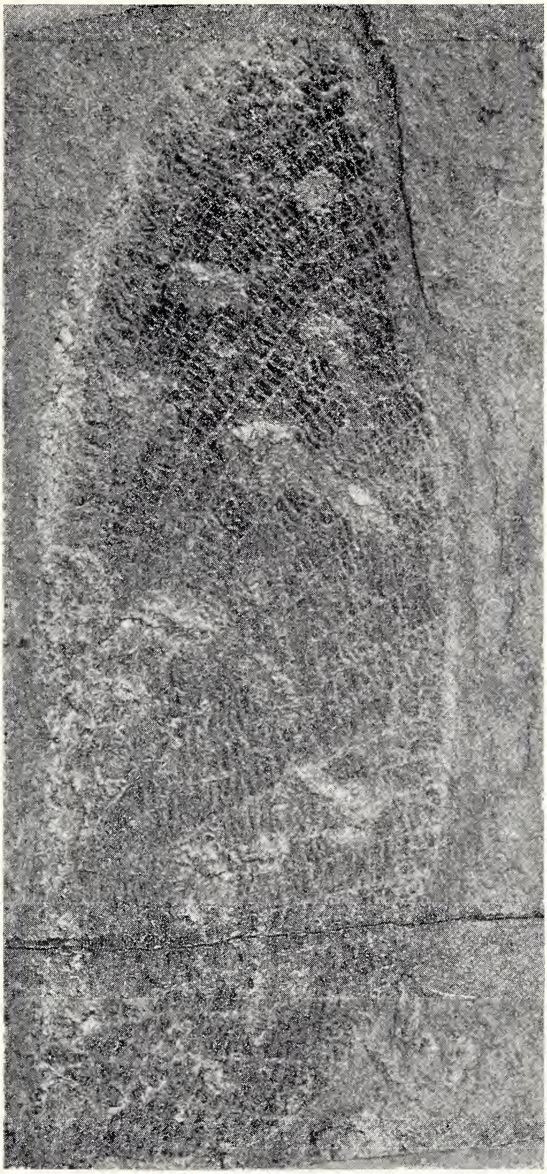
Explanation of Plate 10

Fouquea superba (Meunier). Photograph of holotype, showing pattern of cross veins characteristic of Fouqueidae. Length of wing, 50 mm.



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Palaeodictyoptera (1906) but subsequently (1919) transferred it to the Megasecoptera. This position has been the one generally accepted, although Bolton (1921) retained it in the Palaeodictyoptera.

One of the specimens recently sent to me by Mr. Walter Dabasinskas is a remarkably well preserved wing obviously belonging to the family Brodiidae and close to *Brodia,* but clearly requiring a new genus. The excellent preservation of this fossil has answered some of the questions which have been raised for many years about the Brodiidae. Before describing this new specimen and discussing its affinities, it is necessary to redefine the family Brodiidae on the basis of this additional record and the specimens of *Brodia priscotincta* which I have examined in the British Museum, the U.S. National Museum, and especially in the Scudder collection at the Museum of Comparative Zoology.

The Brodiidae as now known possessed petiolate wings. The costal vein was distinctly serrate on both its anterior and posterior borders; the serrations also extend along the posterior border of the wing, although in general they are smaller and more widely spaced; in some the serrations along the posterior border of the petiole form stout setae; Sc is close to R basally and parellels R1 for most of its length; it apparently merges with the costa somewhat beyond mid-wing but retains its identity until near the apex of the wing (see plate 14); R and R1 are nearly straight until near mid-wing, beyond which R1, which is unbranched, curves slightly away from the costal margin; Rs arises well before mid-wing and forms three or four branches; M arises as an independent vein at the base of the wing, curving slightly posteriorly and forking to produce MA; MA is unbranched and diverges anteriorly towards the origin of Rs, which it very nearly touches; MP divides shortly after the level of the origin of Rs, producing at least two terminal branches; Cu arises as an independent vein at the base of the wing, soon dividing into CuA, which curves slightly anteriorly towards M before turning toward the posterior margin; it is without branches; CuP terminates slightly beyond the origin of Rs. 1 anal vein only is present, this terminating on the posterior margin close to the base of the wing at about the level of the origin of MA. A fine archedictyon may be present over much of the wing surface but true cross veins, sometimes irregular and sometimes nearly straight, occur on certain parts of the wing. Differences in the shape of the fore and hind wings are unknown and the body structure is also unknown.

The family is now represented by two genera: *Brodia,* from the

Upper Carboniferous of England, and *Eubrodia,* new genus, from the Upper Carboniferous of Illinois.

Genus *Brodia* Scudder

Brodia Scudder, 1881, Geol. Mag. **8**: 293.

Wings slender, broadest at about the level of mid-wing; cross veins of two types, a few distinct ones mostly in two irregular series, and an almost uniform pattern of very weak transverse cross veins, very close together, but not forming an archedictyon or a reticulation.

Type-species: *Brodia priscotincta* Scudder

Brodia priscotincta Scudder

Plate 11 and text-fig. 4A

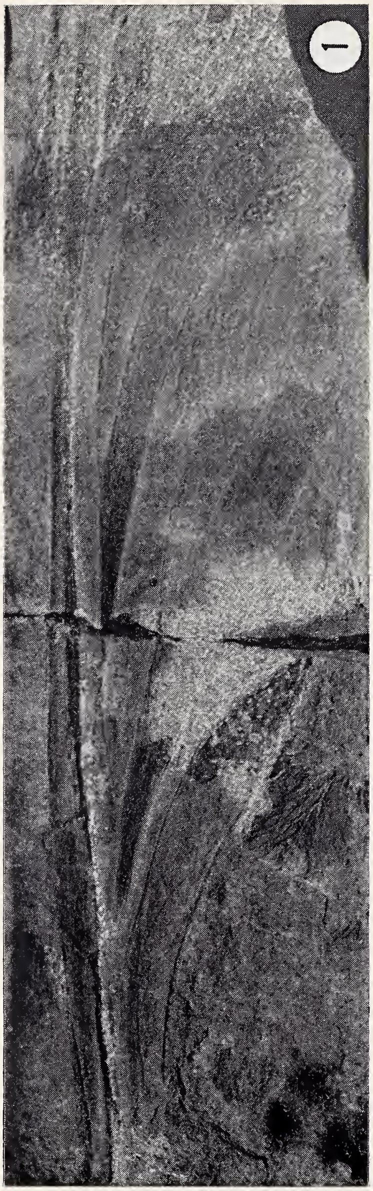
Brodia priscotincta Scudder, 1881, Geol. Mag. **8**: 293; Scudder 1883, Mem. Bost. Soc. Nat. Hist. **3**: 213, pl. 17; Scudder, 1885, in Zittel, Handbuch der Palaeontologie, **2**: 761, fig. 951; Handlirsch, 1906, Foss. Ins., p. 113, pl. 12, fig. 13; Handlirsch, 1919, Denkschr. Akad. Wissensch. Wien, Math.-Naturw. Klasse, **96**: 73-75, figs. 83-89; Bolton, 1921, Foss. Ins. Brit. Coal Meas., **1**: 59-63, figs; Laurentiaux, 1953, in Piveteau, Traité de Paléontologie, **3**: 543, fig. 39.

Synonyms: *Brodia scudderi* Handlirsch, *B. petiolata* Handlirsch, *B. pictipennis, B. fasciata* Handlirsch, *B. nebulosa* Handlirsch, and *B. furcata* Handlirsch (all Handlirsch 1919).

Wing: length 50-58 mm., maximum width, 13-15 mm. Rs with four or five branches; MP usually with two branches, rarely three; a few distinct cross veins in certain areas of the wing, usually transverse or slightly oblique but not reticulate. Wing with three distinct dark transverse bands and a darkened area between R1 and Rs. Type: British Museum (Natural History), Brodie collection No. I.3896. Bolton recorded eleven specimens of *priscotincta* in the British Museum and in the collection at Birmingham University; all of these were from Coseley, Tipton, Sedgeley, or Dudley, Staffordshire, England. Upper Carboniferous (Westphalian).

Several features of this insect, briefly mentioned under the genus and family, require more detailed discussion:

(1) The wing shape. Although Scudder's original figure (1881) of this insect showed a distinct petiolation on the wing, the figure which he published in his more detailed account a few years later (1883) shows much less petiolation and the figure he used in Zittel's Handbuch (1885) shows no petiolation whatsoever. Since all three figures were made from the holotype specimen, we can only conclude that Scudder was not certain of the correct interpretation of the margins of the wing in the specimen. Only a few of the specimens in the British Museum collection show the basal portion of the wing,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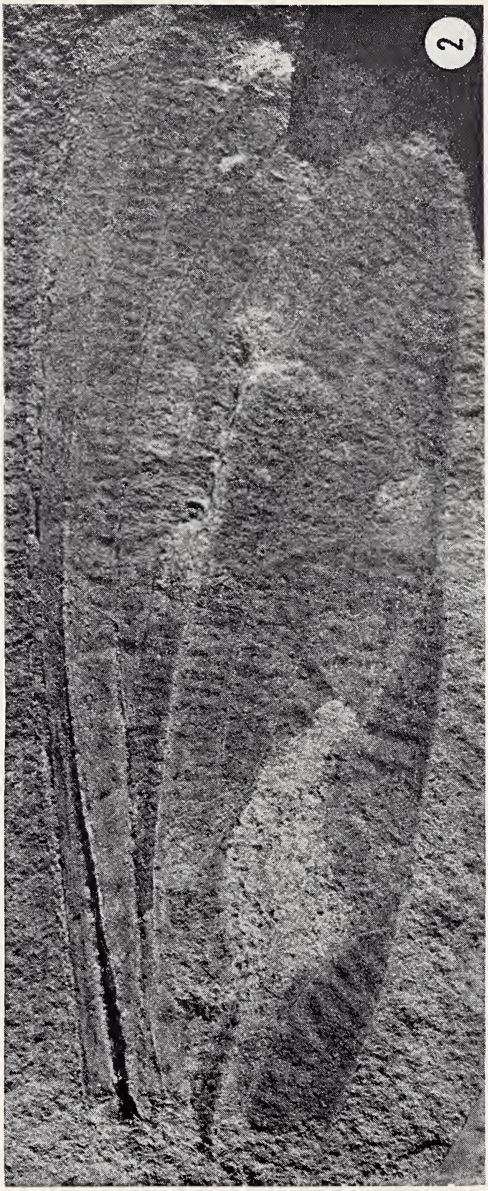
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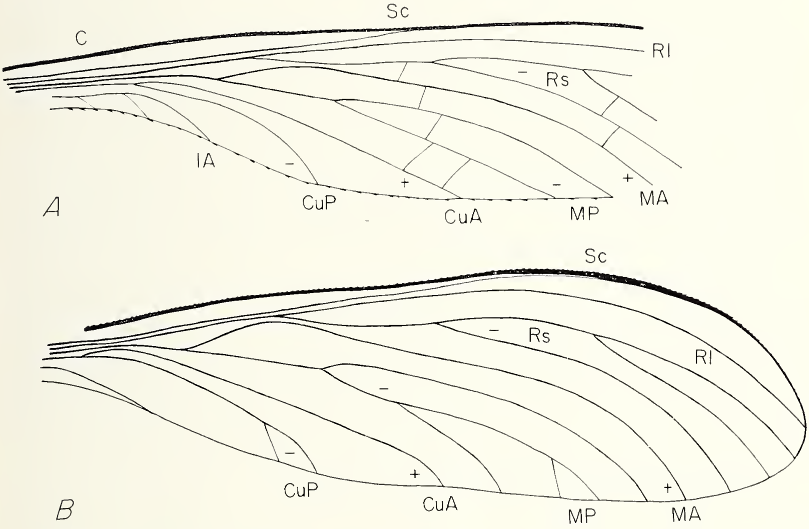
but in all of these the wing base is distinctly petiolate, as shown in Handlirsch's figures (1919). In his diagrammatic representation of the wing, Bolton (1921) shows a subpetiolate condition, in which the wing narrows rather more gradually than depicted in Handlirsch's figures. Although there is probably some slight variation in the degree of petiolation of the wing, I believe that Handlirsch's figures are more nearly correct in respect to this part of the insect. One of the two specimens in the Scudder collection at the Museum of Comparative Zoology shows the petiole distinctly (Plate 11). It is possible, of course, that the fore and hind wings differed in the degree of



Text-fig. 4. Comparison of wings of *Brodia* and *Eubrodia.* A, *Brodia priscotincta* Scudder. Drawing of wing, based on specimens in Scudder Collection, M.C.Z. B, *Eubrodia dabasinskasi,* n. sp. Drawing of wing, based on holotype. The cross-veins and archedictyon are omitted; for these, see plates 12 and 13.

Explanation of Plate 11

Brodia priscotincta Scudder. Upper Carboniferous of England.

Fig.1. Photograph of specimen no. 5842 in M.C.Z. (Scudder Collection), showing the petiole and the transverse, dark bands on the wing. Actual length of wing as preserved, 55 mm.

Fig. 2. Photograph of specimen no. 5843 in M.C.Z. (Scudder Collection), showing the dense pattern of fine cross veins; photographed under very oblique light. Actual length of wing, as preserved, 36 mm.

petiolation but of this we have no information. Bolton figured and described the costal margin at the level of the middle of the petiole as having a distinct hump-like elevation but I have not seen this in any of the specimens which I have examined. There is some uncertainty about the shape of the apex of the wing. Curiously enough, this is missing in all specimens of the species which have been individually described; none of those which were described and figured by Handlirsch and by Bolton show the apex; Bolton includes the apex in his diagrammatic figure of the complete wing but he does not indicate the specimen on which the drawing was based. However, the shape of the wing apex as shown in his "complete wing" is more broadly rounded than that in any specimens which I have seen or which have been described by Handlirsch. The wing represented by Laurentiaux (1953) in an original drawing based upon specimens in the Birmingham Museum has a much more bluntly rounded apex; however, his entire figure seems to be somewhat diagrammatic and is probably not intended to represent the precise form of the wing. The absence of the apical part of the wing in so many specimens suggests that the wings of *Brodia* were unusually fragile and delicate.

(2) The serration of the wing margins. The serrate margin is one of the more obvious features of *Brodia* and it has been figured or mentioned in virtually all accounts of this species. The description and especially the figure given by Scudder in 1883 are accurate and detailed. The structure of the costa is very clearly preserved in the specimens in the M.C.Z. (Scudder collection); they show that the costa has the serrations along both its anterior and posterior edges, those of the anterior edge being somewhat sharper. Beyond the point where the subcosta joins the costa the serrations along the posterior margin of the costa become more pronounced, as correctly drawn by Scudder (see top fig., Plate 14). The subcosta, which is not actually fused or united with the costa, remains visible as an independent vein. In one of the specimens in the Scudder collection the costal margin is very clearly preserved and shows also in the distal part serrations or short spines on the subcosta in that region, making a total three rows of these short projections.[4] It is to be noted in this connection that the radius also bears a few setal bases (see Plate 14). The serrations become very small along the posterior margin distally

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[4] The costal structure of *Brodia* resembles to a striking degree that of the anisopterous Odonata, in which the costa also has serrations on both the anterior and posterior borders.

but the basal part of the hind margin has a few well-developed serrations or heavy stout spines, projecting apically.

(3) The cross veins. These have been the source of considerable confusion. Several distinct cross veins in the pigmented area of the wings have been represented in the drawings of virtually all previous accounts. They appear to be absent from the light or hyaline areas of the wings but I suspect that this is due to the failure of the cross veins to show up in a hyaline area. Bolton was of the opinion, however, that the wing did not, in fact, have color-bands and that the light areas were the result of the wing membrane's being destroyed in those areas. However, the uniformity of the pattern of these dark and light areas in the dozen specimens which have now been found refutes Bolton's theory; furthermore, the presence of the very fine cross veins on the light areas shows that the wing membrane is actually preserved there. The fine indistinct cross veins were noted by Scudder (1883, p. 236) as being "transverse to the nervures they connect, pretty regularly and uniformly distributed over the wing", and Handlirsch (1919) represents them in a few of his figures, although they were not mentioned by Bolton (1921). The effect of these numerous, fine transverse veins is to produce a wrinkled appearance on the wing membrane (see figure 2, plate 11). They are of special significance in view of the presence of a distinct archedictyon in *Eubrodia*; it is my belief that these are vestiges of the archedictyon which are in the process of being lost and replaced by heavier cross veins.

Eubrodia, new genus

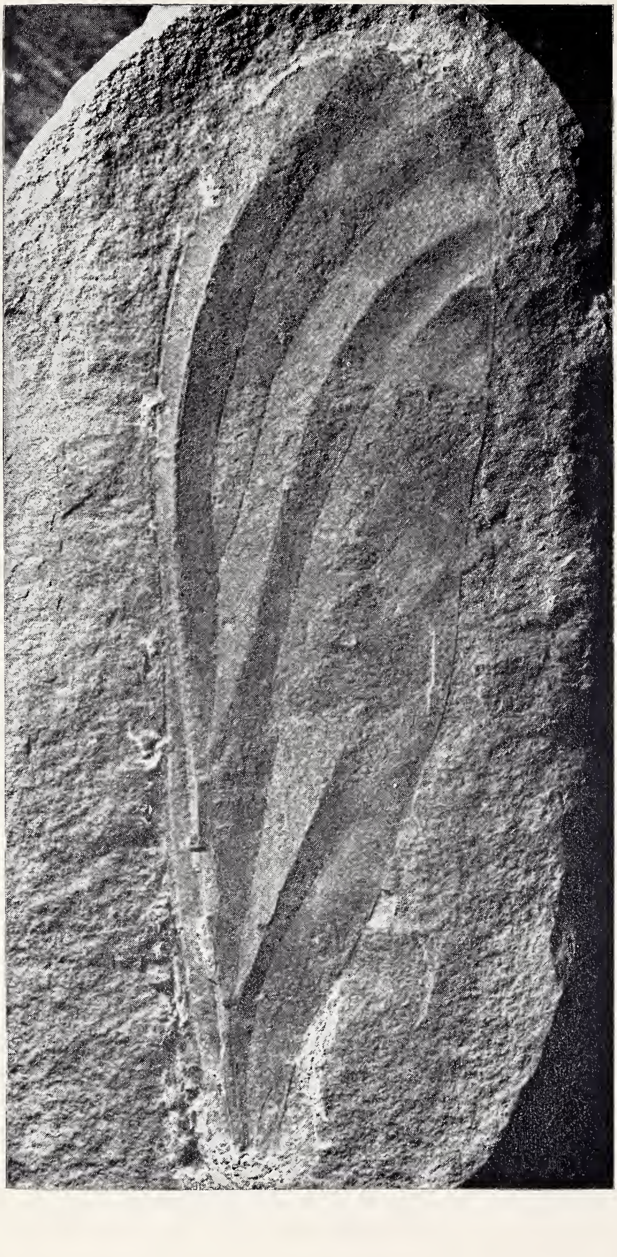
Wing: almost certainly petiolate, as in *Brodia,* but broadest beyond the middle; pattern of main veins much as in *Brodia*; no prominent cross veins as in *Brodia*; a fine archedictyon developed over most areas of the wing; in areas just basal and proximal to the midwing the archedictyon is absent, the cross veins forming a course reticulation.

Type-species: *Eubrodia dabasinskasi,* n. sp.

Eubrodia dabasinskasi, n. sp.

Plates 12 and 13; text-figs. 4B

Wing length as preserved, 48 mm., maximum width, 15 mm.; estimated length of complete wing, 55 mm. The costal margin is slightly concave at about mid-wing, the pterostigmal area being



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noticeably convex; apex of wing posterior to the wing axis; Rs with three terminal branches; MP also with three but with one additional terminal twig on MP3 (probably an individual variation); CuP also with a terminal twig. There is a slight, subtle indication of the presence of two light bands across the wing, one just basal of the mid-wing and the other just beyond the mid-wing, these being in about the same position as the light areas in *Brodia priscotincta*. The details of the venational pattern of the cross veins are shown in plate 13.

Holotype: In the collection of Mr. Walter Dabasinskas, Cicero, Illinois, collected at Pit No. 11, Peabody Coal Company, Section Four, Braidwood, Illinois. The type specimen consists of a virtually complete wing, lacking only the proximal part of the petiole. The preservation is better than that of any other specimen of Brodiidae that I have seen. The species is named for Mr. Dabasinskas in recognition of his efforts and success in collecting insects in the ironstone nodules.

The similarity of the wing of *E. dabasinskasi* to that of *B. priscotincta* is very striking. The obvious differences are in the shape of the wings and in the nature of the cross veins. Additional comments about these and other characteristics of *dabasinskasi* follow.

(1) The wing shape. Comparison of the venational pattern of *dabasinskasi* and *priscotincta* indicates strongly that the wing of *dabasinskasi* was actually petiolate, the petiole being absent in the fossil. The position of 1A and of the point of separation of CuA and CuP in *dabasinskasi* suggests that the wing extended for about the same length as the petiole does in *priscotincta*. Apart from the basal portion, the wing of *dabasinskasi* is noticeably broader distally than that of *priscotincta*. Its shape is very close to that of the supposed nymphal forms of *Brodia* which Bolton described (1921, fig. 16 & 17). As a matter of fact, the shape of the wing of *priscotincta* as shown in Bolton's drawing (figure 15) is much more like that of *dabasinskasi* than it is like the actual specimens of *priscotincta*.[5]

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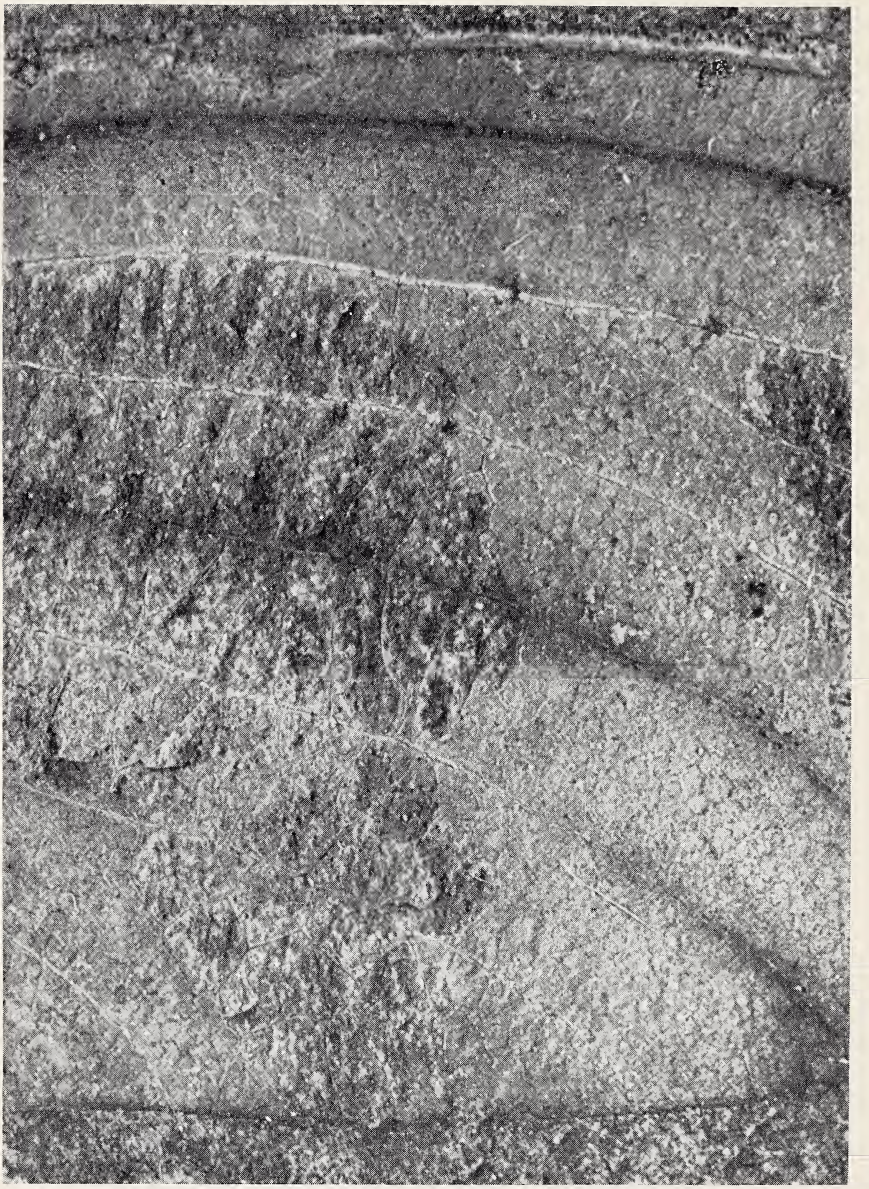
[5] The nymphal wings which Handlirsch described as *Lameereites curvipennis* from the Mazon Creek nodules (1911, p. 375) resemble in general form the nymphal wings described by Bolton as belonging to *Brodia*. There is a good chance that the nymphal *Lameereites* belongs to the family Brodiidae but there is no certainty of it and even less probability that the nymph is the immature form of *Eubrodia*.

EXPLANATION OF PLATE 12

Eubrodia dabasinskasi, n. sp. Photograph of holotype. Length of wing, as preserved, 48 mm.



CARPENTER — CARBONIFEROUS INSECTS

(2) Serrations of the wing margin. These are essentially the same as in *Brodia* but in the pterostigmal region of the wing, the costa is somewhat broadened and the serrations or macrotrichia are larger and more numerous. The subcosta can be seen to continue along the costa towards the apex of the wing and it also bears the short setal processes in the pterostigmal area. (See photograph, bottom fig. plate 14). The radius bears occasional setal bases as in *Brodia* itself. There do not appear to be any heavy setae along the posterior margin, even on the margin near 1A. In this connection it is interesting to note the similarity between the costal margin of *Brodia* and *Eubrodia* and that of *Anchineura,* a megasecopteron from the Upper Carboniferous of Spain (Carpenter, 1963).

(3) The cross veins and archedictyon. These constitute the most distinctive features of *Eubrodia*; the presence of an archedictyon in the Brodiidae is totally unexpected. The archedictyon in *Eubrodia* is a very regular one, present over most of the wing; the individual cells are almost hexagonal in form. In the costal area there are distinctly differentiated transverse veinlets and in the two regions of the wing just basal to the mid-wing and just distal to the midwing, the cross veins form a very different pattern. (See Plate 13). One gets the impression from the structure of the cross veins in *Eubrodia* that the archedictyon is in the process of developing into a more regular and more open reticulation. It now seems probable, from the structure of the wing membrane in *Eubrodia,* that the fine transverse lines in *Brodia,* shown in the photograph (figure 2, plate 11), are vestiges of an archedictyon which was presumably present in the more primitive or ancestral Brodiidae.

Since an archedictyon has not previously been observed in the Megasecoptera, we need to consider the question of whether the Brodiidae are Megasecoptera or Palaeodictyoptera. As noted previously, Handlirsch originally placed *Brodia* in the Palaeodictyoptera and Bolton (1921) persisted in this view. All other students of Palaeozoic insects have placed them in the Megasecoptera or in the Diaphanopterodea. The basic difficulty is that the more we know about the Megasecoptera the more they resemble the Palaeodictyoptera, at least in wing structure (Carpenter, 1963). It may well turn out that we are really dealing with a single order. However,

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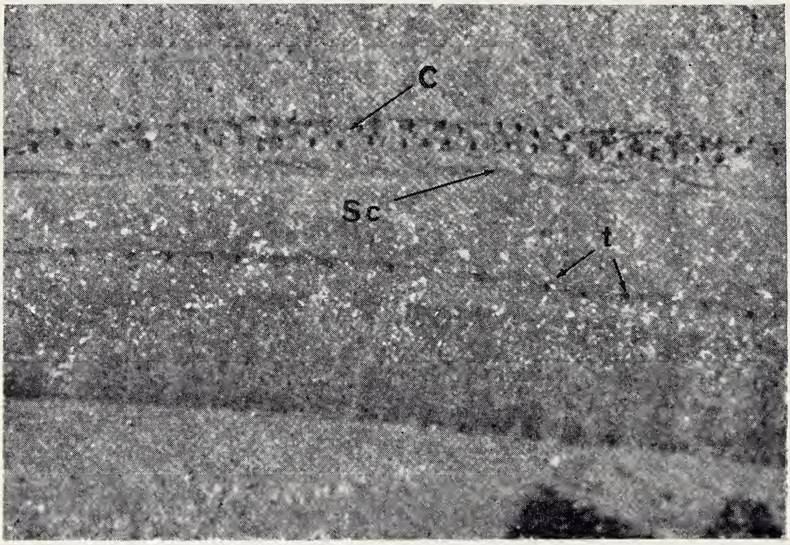
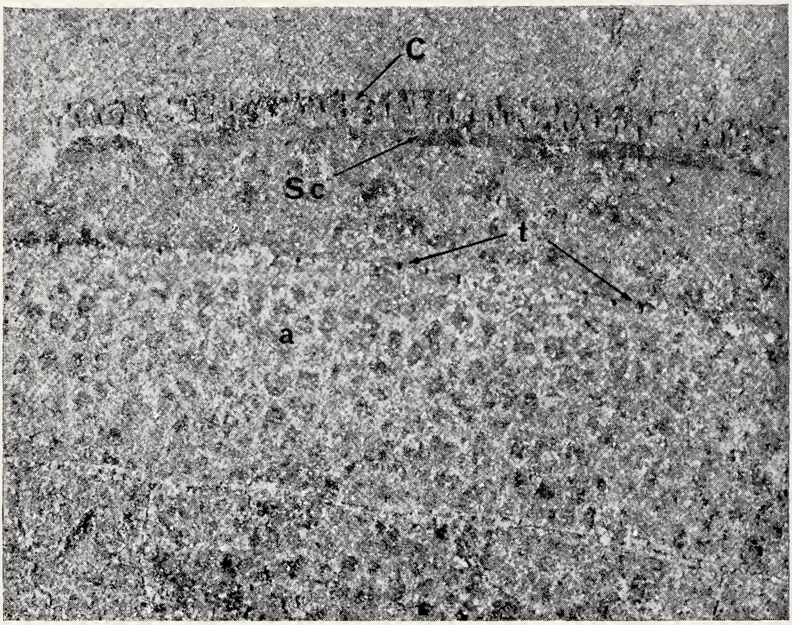
Explanation of Plate 13

Eubrodia dabasinskasi, n. sp. Photograph of middle part of wing (holotype), archedictyon (right side) and longer, irregular cross veins (left side) (times 9).





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we do not know enough about the body structure of the Megasecoptera to permit us to reach a conclusion on the relationship between these two orders. We do not know, for example, whether or not they possessed the prominent beak, now recognized as characteristic of the Palaeodictyoptera. None of the Megasecoptera preserved show a beak but this evidence is negative; the structure of their mouthparts is not actually known. For the present, therefore, it seems advisable to continue to recognize these orders as distinct. The Brodiidae, on the basis of wings, could belong to either of these orders but the evidence is perhaps slightly in favor of the Megasecoptera. At any rate, it seems advisable in the absence of more positive evidence to continue to place the Brodiidae in that order, with the hope that some fortunate collector (perhaps Walter Dabasinskas) will find us a complete specimen of the Brodiidae.

INSECTA INCERTAE SEDIS

Family Sypharopteridae Handlirsch

Sypharoptera pneuma Handlirsch

Text-fig. 5

Sypharoptera pneuma Handlirsch, 1911, p. 372, fig. 55 (Order Sypharopteroidea); Handlirsch, 1921, p. 144, fig. 74; Martynov, 1938, p. 65, fig. 33; Rohdendorf, 1962, p. 69, figs. 106a, b (Order Diaphanopterodea, Suborder Protodiaphanopterodea); Laurentiaux, 1953, p. 426 (Sypharopterodea).

The specimen on which this species was based consists of four wings and part of the thorax and abdomen, the wings being directed backwards, obliquely along the abodmen. Since Handlirsch was unable to assign this fossil to any known order, extinct or Recent, he established a new one for it, the Sypharopteroidea, which he thought represented an extinct off-shoot of the Palaeodictyoptera, with possible relationship to the Megasecoptera. In 1921 he published a restored figure of the complete insect, showing the details of the head (including antennae and eyes) and legs, although none of these were

---

EXPLANATION OF PLATE 14

Top figure, *Brodia priscotincta* Scudder. Photograph of part of wing in pterostigmal area (times 13); specimen in Scudder Collection, M.C.Z.

Bottom figure, *Eubrodia dabasinskasi*, n. sp. Photograph of part of wing in pterostigmal area (times 13), holotype.

Explanation of lettering: C, costa; Sc, subcosta; t, setal bases on R1; a, archedictyon of *Eubrodia*. The costa shows the prominent setae that form the serrations.

preserved in the single specimen known. Martynov (1938) faced with the problem of placing the insect in either his Palaeoptera or Neoptera, came to the conclusion that *Sypharoptera* was palaeopterous, assuming the flexed position of the wings as due to abnormal positioning at the time of preservation in the fossil state. He was also of the opinion that *Sypharoptera* was more similar to the Spilapteridae (Palaeodictyoptera) than to the Megasecoptera. Laurentiaux (1953) accepted this view but Rohdendorf (1962) placed *Sypharoptera* in the palaeopterous Order Diaphanopterodea, regarding the flexed wings as being in normal position.

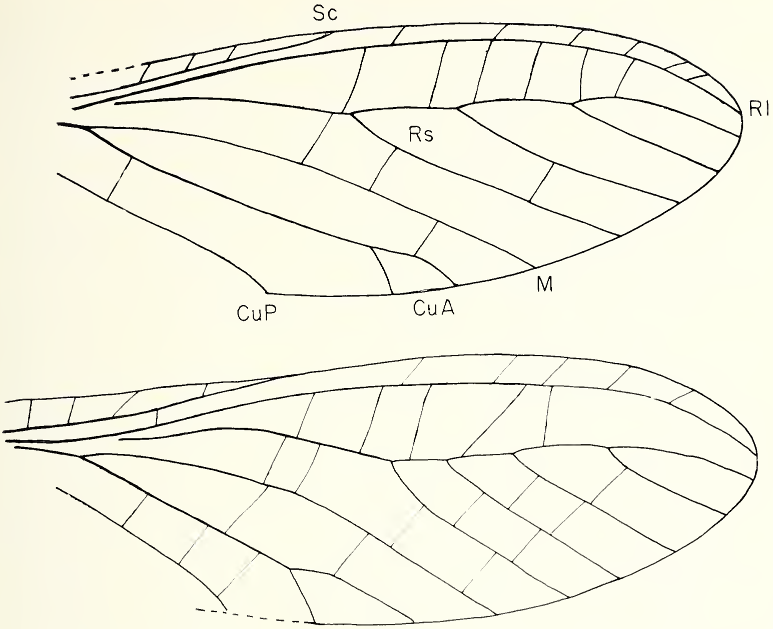
Recently, through the kindness of the authorities at the Peabody Museum at Yale University, I have had the opportunity of studying this puzzling fossil. Since my interpretation differs from that of previous workers, I include here a new formal description of it and a discussion of its probable relationships.

The specimen is a small one, the fore wing of the type being 10 mm. long. Although the fore and hind wings are overlapped on each side of the abdomen, their venational pattern has been worked out without too much difficulty.[6] The results of my efforts to untangle the veins are shown in text-figure 5, which differs only slightly from that of Handlirsch (1911): in both wings, in my opinion, M arises from CuA, and not as an independent vein from the base of the wing, as shown by Handlirsch. This origin of M can be demonstrated in the fossil by the use of ammonium chloride and also by wetting the specimen with alcohol or water.

The subcosta terminates at about mid-wing, apparently on the costal margin; R1, which is strongly convex, is close to and about parallel to the anterior margin for most of its length; there are several oblique veinlets between R1 and the costa; R1, which is clearly concave, arises from R well before mid-wing and is directed away from R1 distally, giving rise to four or five pectinate branches; the wide space between Rs and R1 distally has several long, oblique veinlets; M, as noted, arises from CuA near the wing base, slightly before the origin of Rs; this is a *simple vein without branches* and it is neutral in its topography, *neither convex nor concave*, and is here designated as M; two branches of Cu are preserved in the fossil;

---

[6] This was done by the aid of photographic enlargements of the wings. The two sets of veins (those of each overlapped wing) were traced with inks of different colors, following the precise connections or deviations of each vein. Eventually the veins of each color were traced on separate sheets of thin paper.



Text-fig. 5. *Sypharoptera pneuma* Handlirsch. Drawing of wings, based on holotype, Peabody Museum, Yale University. CuA is strongly convex; M is neutral.

CuA, which is strongly convex, gives rise to M and also to a short distal fork; CuP is concave and unbranched. The anal region is not preserved in either fore or hind wing.

Very little of the body structures are actually visible in the fossil. Handlirsch's figure (1911) shows some details which I am unable to discern in the specimen, such as the subdivisions of the meso- and metathorax and the complete segmentation of the abdomen. At the end of the latter there are two very short cerci, consisting of two or possibly three segments; these are close together and were apparently interpreted by Handlirsch as forming a short ovipositor; these appendages are very small, only one-half millimeter in length, but the segmentation can distinctly be seen.

The venational pattern is the same in the fore and hind wings of *Sypharoptera,* at least in those parts of the wings which are preserved; the presence of an additional branch on Rs in one wing must be an individual wing variation, for it does not exist in the other hind wing of the specimen. The costal area of what appears to be the fore wing seems, curiously enough, to be somewhat more narrow than that of the hind wing but no other differences are apparent. The most striking feature of the wings is the presence of a single media, which is unbranched and which is neutral in its position. This would seem to me, without any question, to eliminate *Sypharoptera* entirely from the Palaeoptera, which retain the convexity or concavity of the branches of M to a very marked degree. On the other hand, this condition of M is one which occurs in various groups of the Neoptera; and, of course, the position of the wings is neopterous. What is not known, unfortunately, is whether or not the hind wing possessed an expanded or enlarged anal area. In the hind wing of the fossil (and in the fore wing also for that matter) the anal area is completely missing. It seems to me, therefore, that the bulk of the evidence, such as it is, points to the conclusion that *Sypharoptera* is not palaeopterous as it was treated by Martynov, Rohdendorf and Laurentiaux, but neopterous.

Within the great group of neopterous orders, the position of *Sypharoptera* is not at all clear on the basis of its venation; and the very short cerci are no real help. It seems to me, therefore, that the family Sypharopteridae should be placed in the category of the Insecta Incertae Sedis. Handlirsch's policy of erecting new orders for fragmentary fossils which he could not fit into known groups has no justification. He indicated that he was establishing orders "provisionally" but the meaning of that term is not clear, since all taxonomy is provisional, in the sense that changes may be made by subsequent investigators. The main disadvantage of the procedure followed by Handlirsch is that many meaningless, ordinal names are introduced into the literature, thus confusing the concept of the really extinct and valid orders. Until something is known of the body structure, including the mouth-parts, and the differences in the fore and hind wings, I consider it useless to establish separate orders for fossils. Accordingly, I am placing *Sypharoptera* in the category of Insecta Incertae Sedis; the name Sypharopterodea (or Sypharopteroidea as originally used by Handlirsch) remains associated with this insect as the *nomen* of a higher category, the nature of which will be determined after specimens have been found that provide enough information for definite conclusions.

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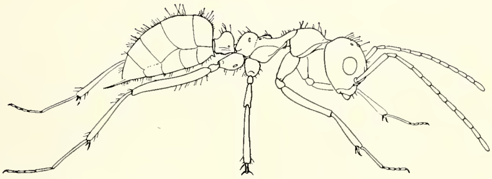

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PSYCHE

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THE EVOLUTIONARY SIGNIFICANCE OF ROTATION OF THE OÖTHECA IN THE BLATTARIA

By Louis M. Roth
Pioneering Research Division
U.S. Army Natick Laboratories, Natick, Mass.

The newly-formed oötheca of all cockroaches projects from the female in a vertical position, with the keel and micropylar ends of the eggs dorsally oriented. All of the Blattoidea (Fig. 1) and some of the Blaberoidea carry the egg case without changing this position. However, in some of the Polyphagidae (Figs. 11-16) and Blattellidae (Figs. 2,3), and all of the Blaberidae, the female rotates the oötheca 90° so that the keel faces laterally at the time it is deposited on a substrate (Polyphagidae, Blattellidae), carried for the entire embryogenetic period (*Blattella* spp.), or retracted into the uterus (all Blaberidae). According to McKittrick (1964), rotation of the oötheca frees the keel from the valve bases which block an anterior movement of the oötheca while it is in a vertical position, and it orients the oötheca so that its height lies in the plane of the cockroach's width, thus making it possible to move the egg case anteriorly beyond the valve. It is likely that by the time the oötheca had evolved to the stage where it was retracted internally, the height of the keel had been greatly reduced (e.g., in *Blattella* spp.) and it would not be necessary to free its keel from the valve bases. The eggs of Blaberidae increase greatly in size in the uterus during embryogenesis (Roth and Willis, 1955a, 1955b). A logical advantage for rotating the oötheca prior to retraction resulted in orienting the eggs in the female's body in a position which would permit the uterus to increase in size as the embryos developed. When stretched by a newly deposited oötheca, the uterus of a blaberid presses against the inner surfaces of the tergum and sternum but there is lateral room for expansion. If the oötheca was not rotated prior to retraction, the long axes of the eggs would lie vertically and during gestation the uterus would have to stretch dorso-ventrally, a direction which allows little room for expansion in these relatively flat insects.

Manuscript received by the editor December 15, 1966

Hebard (1919) described a specimen of *Lissoblatta flabellata* (Saussure) which was carrying a partially extruded oötheca in a horizontal position, and another female of the same species with an oötheca that was slightly less extruded than the above specimen but with the suture dorsad. Hebard concluded that "The position in which the oötheca is carried would, from this evidence, again appear to have little or no significance in systematic work in the Blattidae." Unfortunately, this conclusion was based on how the oötheca happened to be carried when the female was collected and preserved. This is also true of Karny's (1924) and Bey-Bienko's (1950) observations that the oötheca of *Ectobius* is carried with the keel upright; prior to its deposition the oötheca is rotated in species of this genus (Brown, 1952; Roth and Willis, 1957).

The manner in which the oötheca is carried while it is being formed is unimportant taxonomically since it is the same in all cockroaches. How the egg case is carried at the time it is being deposited is significant taxonomically and important for understanding the evolution of ovoviviparity and viviparity. Dried museum specimens cannot always be used to determine whether or not rotation of the oötheca takes place. If, in a museum specimen, the oötheca is carried vertically in the vestibulum, it does not necessarily mean that this is its position when it is deposited. The danger of using museum specimens in determining rotation was emphasized when I examined specimens in the Rehn and Hebard collection at The Academy of Natural Sciences of Philadelphia. A specimen of *Cariblatta minima* Hebard had the oötheca oriented with the keel laterad. This may have been the specimen which Hebard (1917) used in claiming that *C. minima* rotated its egg case. It was apparent that the egg case had been glued on the female, and in doing so it was reoriented when inserted into the female's vestibulum. Roth and Willis (1954) found, by observing living females, that the oötheca of *Cariblatta* is not rotated prior to

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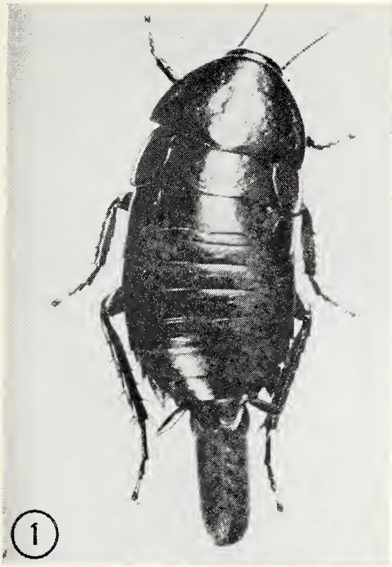
Explanation of Plate 15

Figures 1-4. Females of Blattaria carrying oöthecae. Fig. 1. *Maoriblatta novae-seelandiae* (Brunner) (Blattidae) (formerly *Platyzosteria novae-seelandiae* Brunner; Princis, 1966). No rotation, (× 2.0). Fig. 2. *Ischnoptera deropeltiformis* (Blattellidae: Blattellinae). Advanced rotation, (× 3.6). Fig. 3. *Blattella germanica* (Blattellidae: Blattellinae). Advanced rotation, (*ca* × 4.9). Fig. 4. *Dendroblatta sobrina* (Blattellidae: Plectopterinae). Aberrant "rotation" resulting from the female having difficulty in depositing the oötheca. This species does not normally rotate its oötheca. (× 5.7)

(Figs. 1 and 2 from Roth and Willis, 1960)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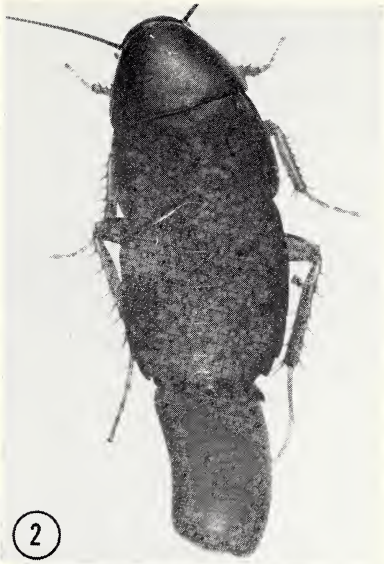
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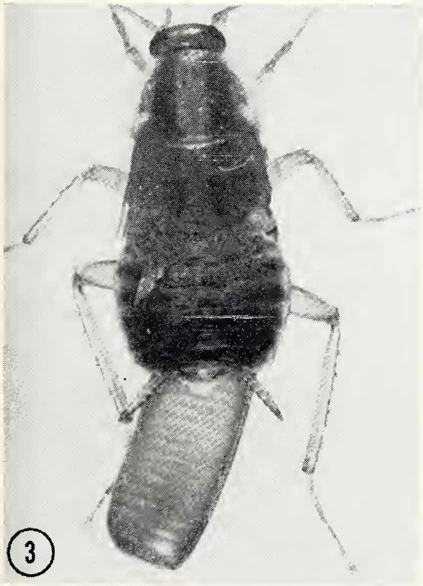
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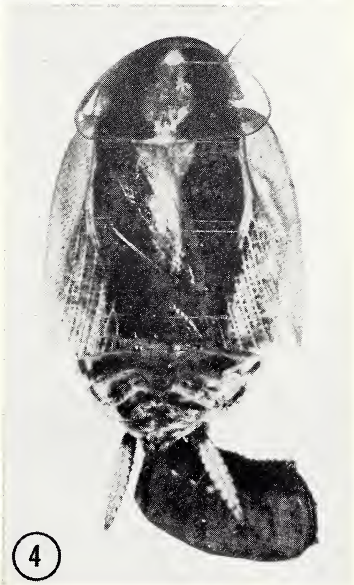
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ROTH — BLATTARIA

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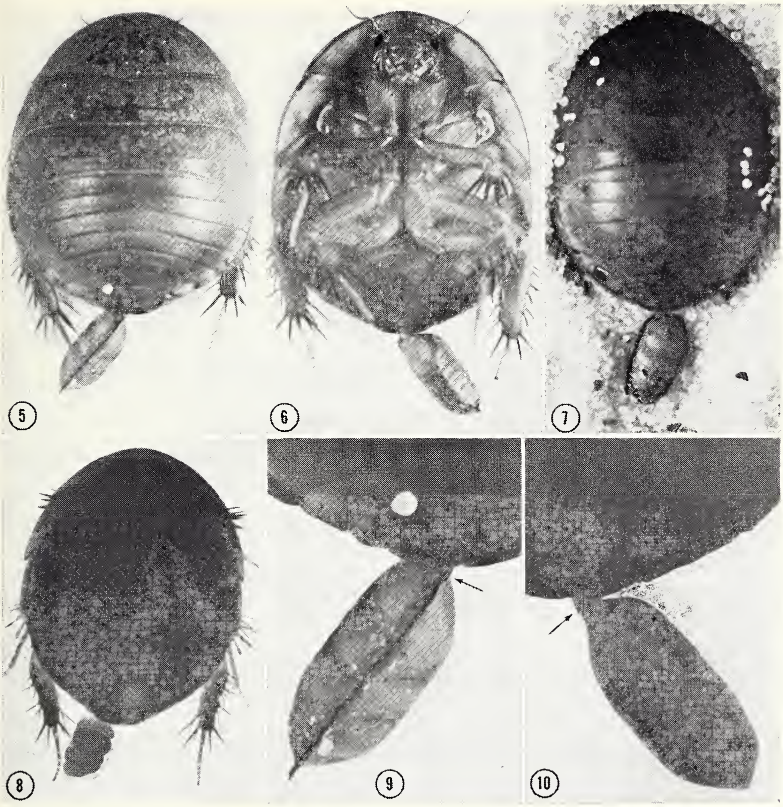
deposition. At the Academy, I also saw pinned specimens of *Dendroblatta sobrina* Rehn (Plectopterinae), *Chorisoneura barticae* Hebard (Plectopterinae), and *Periplaneta brunnea* Burmeister (Blattinae), each bearing an oötheca with the keels facing laterad. These genera do not normally rotate their oöthecae (see below). In the *Chorisoneura* female the abdomen was obviously abnormally flattened and the oötheca must have been "rotated" artificially when this occurred.

Rotation of the oötheca is an important behavioral taxonomic character in the Blattellidae and may be used to separate the nonrotators (Anaplectinae and Plectopterinae) from the rotators (Blattellinae, Ectobiinae, and Nyctiborinae) (McKittrick, 1964). The absence of rotation led to a study which resulted in the erection of 2 new genera, *Agmoblatta* and *Isoldaia,* of Plectopterinae; these were formerly Blattellinae, in the genus *Loboptera* (Gurney and Roth, 1966). According to Hebard (1919) *Lissoblatta flabellata* rotates its oötheca. Princis (personal communication) claims that *Lissoblatta* is a synonym of *Riatia.* McKittrick (1964) placed *Riatia* in the nonrotating Plectopterinae. Hebard may have erred in his interpretation of the position in which the oötheca was carried, or the generic placement of this genus requires additional study.

I place the following species, whose genera are included in the Blattellidae (Princis, 1960) in the Plectopterinae because the females do not rotate their oöthecae: *Dendroblatta sobrina, Ellipsidion affine* Hebard, *Euphyllodromia angustata* (Latreille), *Latiblattella* sp. nov. I would also place *Celeriblattina* Johns in this subfamily because, according to Johns (personal communication), it does not rotate its oötheca. The following Blattellidae (Princis, 1960) rotate their oöthecae and I include them in the Blattellinae: *Chorisia fulvotestacea* Princis, *Gislenia australica* (Brunner), *Ischnoptera rufa rufa* (Degeer), *I. panamae* Hebard, *I. deropeltiformis* (Brunner), and *Nesomylacris relica* Rehn and Hebard; the following have been reported to rotate their oöthecae and are therefore included in the Blattellinae: *Loboptera decipiens (Germar)* (Lefeuvre, 1959, Gurney and Roth, 1966), *Lobopterella dimidiatipes* (Bolívar) (McKittrick, 1964, as *Loboptera;* Princis (1957) used *Loboptera dimidiatipes* to erect *Lobopterella*), *Tartaroblatta* Bey-Bienko (Bey-Bienko, 1950), *Ignabolivaria* Chopard (Bey-Bienko, 1950), *Aristiger histrio* (Burmeister) (Karny, 1924, as *Hemithyrsocera histrio;* Princis (personal communication) says that this species is now *Aristiger histrio*), and *Parellipsidion* Johns (Johns, 1966).

I have seen very few instances of "rotation" in Plectopterinae. One female of *Dendroblatta sobrina* (Fig. 4) and 2 females of *Lopho-*



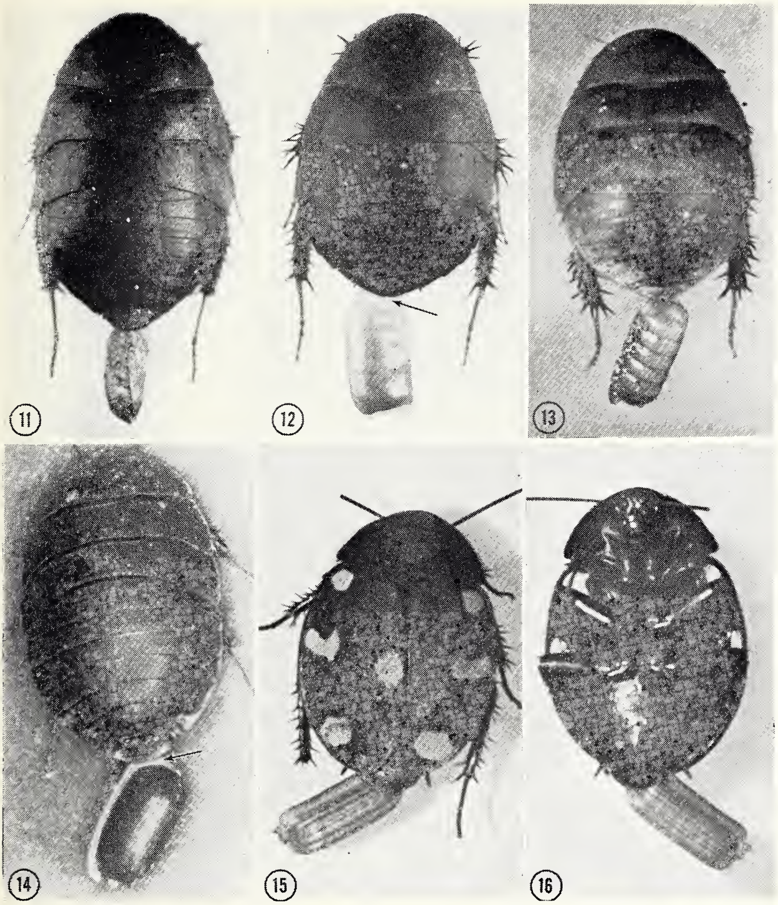
Figures 5-10. *Arenivaga (Psammoblatta) cerverae* carrying a completely formed oötheca. Fig. 5. Dorsal view, (× 2.1). Fig. 6. Ventral view, (× 2.1). Fig. 7. Dorsal view of a female in sand; the oötheca is twisted so that the keel faces to the left, (× 2.2). Fig. 8. Dorsal view; light coming from below showing the eggs visible inside the oötheca. Note that the anterior eggs do not lie in the vestibulum, (× 1.9). Figs. 9-10. Enlarged views of the oötheca shown in figures 1 and 2; note the flange (arrows) held securely in a vertical position by the paraprocts. (× 5.3)

blatta sp. nov. rotated their oöthecae but these were instances in which the females apparently had difficulty in dropping the egg cases.

I have observed many females of the desert polyphagid, *Arenivaga (Psammoblatta) cerverae* (Bolívar) oviposit. Sometimes the oötheca was oriented with the keel laterad (Figs. 7,8) but this was not because they had been rotated. The oötheca of *A. cerverae* has a long flange (Figs. 17,19) or "handle" which is held vertically between the parapracts (i.e., the flat surface of the flange is in a vertical plane) (Figs. 9,10). When the female is on a sandy substrate, she tends to sink into the sand particles, and because the flexible flange is twisted, the oötheca may be held with the keel laterad (Fig. 7). If the female is raised off the substrate the oötheca hangs in its normal position with the suture dorsad (Figs. 5,6).

Although Alfieri (1921) briefly described and illustrated the oötheca of *Polyphaga aegyptiaca* (Linnaeus), he did not mention whether or not it was rotated prior to its deposition. At the Philadelphia Academy I saw a female specimen of *P. aegyptiaca* with an oötheca on the same pin. The collection data stated "Alive and bearing oötheca horizontally in raw opium from Smyrna, Asia Minor. At Quarantine Port of New York — VII-3-1919, H. B. Shaw." In our laboratory culture I have seen females of *P. aegyptiaca* carrying oöthecae more than a dozen times. In only 3 instances were the egg cases carried with the keel laterad and this was apparently not normal. The oötheca of *P. aegyptiaca* also has a flange (cf. Figs. 17 and 18) by which it is held in the paraprocts. However, the flange is relatively shorter and more rigid than that found in *A. cerverae*. The supra anal plate of the female of *P. aegyptiaca* has a median cleft in it, and the very high keel (Fig. 18) of the extruded egg case lies between the margins of this indentation; this helps to support the oötheca in a vertical position. When the female is jostled by other individuals in the culture, or for other reasons, the keel may be disengaged from the cleft of the supra anal plate. Because the oötheca is not firmly inserted but is held by a flange between soft paraprocts, the large egg case may fall on its side. When in this position, one can be misled into thinking that rotation has occurred. The twisted oötheca can be turned upright easily without disengaging it from the female indicating the flexible nature of how it is held. The oötheca of *Polyphaga saussurei* (Dohrn) and *P. indica* Walker have flanges (Bey-Bienko, 1950) somewhat similar to that of *P. aegyptiaca*. The egg case of *Euthyrrapha pacifica* (Coquebert) (Fig. 20) also has an elongated flange which is probably flexible, but nothing is known about the oviposition behavior of this species.

In the polyphagids, *Arenivaga (Arenivaga)* spp. (Figs. 11-13), the female rotates the oötheca in a manner similar to that figured by McKittrick (1964) in *Arenivaga (Arenivaga) bolliana* (Saussure) (Fig. 14). However, McKittrick (1964) did not consider this to be rotation because once rotated, the oötheca is attached to the female only by a flange (Figs. 12,14 arrows) and none of the eggs are hidden within the vestibule (McKittrick, personal communication).



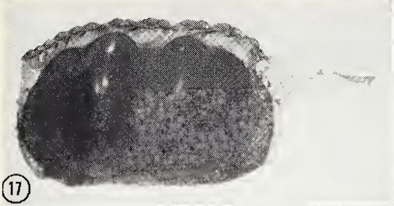
Figures 11-16. Primitive rotation of the oötheca in the Polyphagidae. Figs. 11-12. *Arenivaga (Arenivaga)* sp. *A* (Kelso Dunes, California). Fig. 11. Oötheca being formed and still in the vertical position. Fig. 12. Oötheca rotated with keel to right, (× 2.8). Fig. 13. *Arenivaga (Arenivaga)* sp. *B* (Coachella Valley, California). Oötheca rotated with keel toward left. Note the flange by which the oötheca is held and that none of the eggs are hidden in the vestibulum, (× 2.0). Fig. 14. *Arenivaga (Arenivaga) bolliana*. Oötheca rotated toward left. (From McKittrick, 1964; courtesy of Dr. F. A. McKittrick), (*ca.* × 1.9). Figs. 15-16. *Therea petiveriana* (India). Oötheca rotated to left. 15. Dorsal view. 16. Ventral view, (× 1.6).

(Arrows in Figs. 12 and 14 point to flange by which the oötheca is held between the paraprocts).

The flanges of the oöthecae of the subgenus *Arenivaga* (Figs. 21-23) are considerably shorter than the flanges of the subgenus *Psammoblatta* (Figs. 17,19) or of *Polyphaga aegyptiaca* (Fig. 18), and suggest that within the Polyphagidae there has been a reduction in the length of the flange. According to McKittrick (1964) the oöthecae of some of the more primitive Plectopterinae still have a flange.

Since rotation is defined as a reorientation or turning of the oötheca 90° so that the keel faces laterally, I consider the manner in which *Arenivaga (Arenivaga)* spp. carry their egg cases prior to depositing them, as true rotation. However, this may be considered to be a primitive type of rotation because none of the eggs are enclosed or hidden within the vestibulum of the female after the egg case is turned 90°. The polyphagid *Therea petiveriana* (Linnaeus) also rotates its oötheca (Figs. 15,16) prior to depositing it, as figured by Ananthasubramanian and Ananthakrishnan (1959). Because of the supra-anal plate, it appears as though some of the anterior eggs are within the vestibulum of the female (Fig. 15). However, when viewed ventrally (Fig. 16) one can see that none of the eggs are hidden inside the female. The flattened upper anterior corner of the oötheca (Fig. 24) is the only part held by the female. McKittrick (1964) claims that the polyphagid *Hypercompsa fieberi* (Brunner) does not rotate its oötheca. However, she (personal communication) based this conclusion on a preserved female that was carrying a fully formed oötheca with the keel upright. This female may have been preserved prior to rotating the oötheca and a definite conclusion as to whether or not the Holocompsinae rotate the oötheca must await study of additional material.

Bey-Bienko (1950) erected three subgenera of *Arenivaga;* he believed that the subgenus *Arenivaga* (restricted in distribution to the deserts of the southwestern part of North America and with one species peculiar to the peninsula of Florida) is very close to and is an unquestioned derivative of the subgenus *Psammoblatta,* but is more specialized than the latter. The method of oviposition (i.e., rotation) tends to support Bey-Bienko's conclusion that *A. (Arenivaga)* is more advanced than *A. (Psammoblatta)*. The Polyphagidae need revision, using characters studied by McKittrick (1964). I sent specimens of *Arenivaga (Psammoblatta) cerverae* to McKittrick, and she believes that it is not an *Arenivaga* and does not think it belongs in the Polyphaginae (where she includes *Arenivaga (Arenivaga)* spp.). She wrote (personal communication) that *A.* (*P.*) *cerverae* is close to the Polyphaginae; the female genitalia ". . . are in general arranged like those of *Arenivaga* (*A.*) *bolliana,* and *A.*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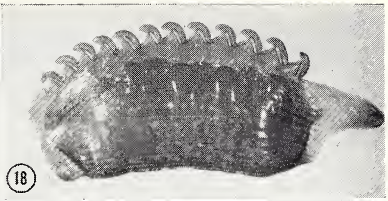
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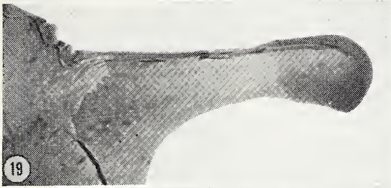
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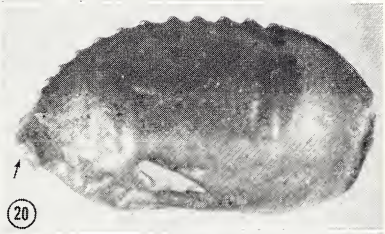
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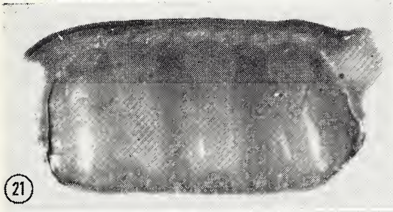
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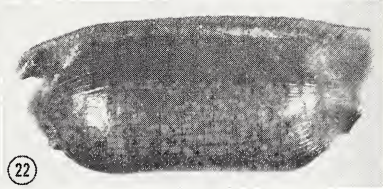
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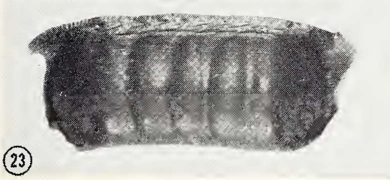
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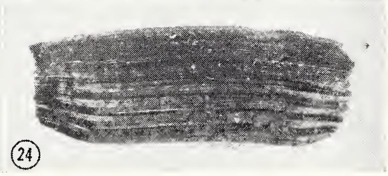
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Figures 17-24. Oöthecae of Polyphagidae. Fig. 17. *Arenivaga (Psammoblatta) cerverae,* (× 2.0). Fig. 18. *Polyphaga aegyptiaca,* (× 3.6). Fig. 19. Flange of *A. (P.) cerverae,* (× 17.6). Fig. 20. *Euthyrrhapha pacifica,* (× 11.0) (Arrow points to flange which is twisted laterally). Fig. 21. *Arenivaga (Arenivaga)* sp. *A.* (× 6.8). Fig. 22. *Arenivaga (Arenivaga) bolliana.* (× 4.2). Fig. 23. *Arenivaga (Arenivaga)* sp. *B.* (× 4.7). Fig. 24. *Therea petiveriana,* (× 3.4).

(In figures 21-23 the flattened flange is on the right side and in figure 24 it is on the left.)

(*A.*) *apacha,* but are quite different in several particulars. . . . The proventriculus is more like that of *Polyphaga aegyptiaca* than that of *Arenivaga apacha.*" The fact that *A. (Psammoblatta) cerverae* does not rotate its oötheca whereas species of the subgenus *Arenivaga* do, lends support to McKittrick's view that these should be in different subfamilies and probably should be different genera. A detailed study of the oviposition behavior and structure of the oöthecae of polyphagids may have considerable value in the taxonomy of the Polyphagidae and should add considerably to our knowledge of the evolution of the egg case in the Blattaria.

I consider the rotation of the oötheca as it is found in the Blattellidae (Blattellinae, Ectobiinae, and Nyctiborinae) and all of the Blaberidae to be an advanced type, because once rotated, the anterior eggs (those leaving the oviduct last) covered by the oöthecal membrane are in close contact with tissues in the female's vestibulum (Figs. 2,3). This contact was essential for the evolution of ovoviviparity and viviparity, because in species like *Blattella,* the eggs obtain water from the female while the oötheca is carried externally during embryogenesis. I have seen a female of *Chorisia fulvotestacea* Princis carrying a transparent oötheca, with the keel laterad, containing well developed embryos. The oötheca of *Chorisia* is also very similar to *Blattella.*

Shelford (1913) noted that a female of *Temnopteryx abyssinica* Saussure and Zehntner was carrying an oötheca with the keel directed to one side, and the egg case was so transparent that the eyes of the enclosed embryos were visible. This type of oviposition would be similar to that found in *Blattella* and *Chorisia.* Shelford placed *T. abyssinica* in synonymy with *Hemithyrsocera circumcincta* (Reiche and Fairmaire). Rehn (1933) made *Blatta circumcincta* R. and F. the type of the genus *Burchellia.* Princis (1962) placed *Burchellia* in the Ectobiidae (this would probably be the Ectobiinae in McKittrick's (1964) classification). As far as I know none of the Ectobiinae have transparent oöthecae that are carried for the entire embryogenetic period. Princis (personal communication) states that "Whether Shelford was correct in synonymizing *Temnopteryx abyssinica* Sauss. and Zhnt. under *Burchellia circumcincta* (R. and F.) is somewhat doubtful. Although Shelford had examined the type of *abyssinica,* he placed the species under *B. circumcincta* with a query. It seems that Shelford himself was uncertain."

In discussing oviposition by present day oviparous cockroaches, Laurentiaux (1959) stated that the oötheca is generally carried for a month or longer attached to the female before she abandons it. This is not true for most oviparous species which drop their oöthecae within a few days after forming them. Carrying the oötheca during the entire embryogenetic period can be considered to be the most advanced type of oviposition behavior among oviparous Blattaria and is comparatively rare (at present this is known to occur only in *Blattella* and *Chorisia*).

TABLE 1. — DIRECTION OF ROTATION OF OÖTHECAE IN DIFFERENT SPECIES OF POLYPHAGIDAE AND BLATTELLIDAE

	Number of Oöthecae Rotated to:		
Species	Left	Right	Source[a]
Polyphagidae			
Arenivaga (Arenivaga) sp. *A*	0	1	
Arenivaga (Arenivaga) sp. *B*	3	1	
Arenivaga (Arenivaga) bolliana (Saussure)	1	0	McKittrick (1964)[b]
Therea petiveriana (Linnaeus)	3[c]	3[d]	
Blattellidae			
Blattellinae			
Blattella germanica (Linnaeus)	?[h]	usual	Gould and Deay (1938)
	0	?	Blochmann (1887)
	0	?	Ross (1929)
	0	1	Pope (1953)
	few	usual	Willis *et al.* (1958)
	0	49	Wheeler (1889)
	3	97	Wille (1920)
	6[c]	62	
Blattella humbertiana (Saussure)	0	27	
Blattella unicolor (Brunner)	0	20	
Blattella vaga Hebard	few	usual	Willis *et al.* (1958)
Ischnoptera deropeltiformis (Brunner)	2[c]	18	
Ischnoptera panamae Hebard	6[d][m]	34	
Ischnoptera rufa rufa (Degeer)	33	78	
Loboptera decipiens (Germar)	0	2	
	0	?	Lefeuvre (1959)
Parcoblatta pensylvanica (Degeer)	3[c]	8[c]	
Parcoblatta uhleriana (Saussure)	0	1	
Parcoblatta virginica Brunner	0	1	McKittrick (1964)[b]
Pseudomops septentrionalis Hebard	1	0	McKittrick (1964)[b]
Shawella couloniana (Saussure)	3[d][s]	75	
Symploce hospes (Perkins)	4[c]	111	
Tartaroblatta tartara (Saussure)	0	?	Bey-Bienko (1950)
Tartaroblatta karatavica Bey-Bienko	0	?	Bey-Bienko (1950)
Xestoblatta immaculata Hebard	2[c]	24	
Ectobiinae			
Ectobius pallidus (Olivier)	0	19	Roth and Willis (1957)
Ectobius panzeri Stephens	27	3	Brown (1952)

[a]) Where no reference is given the observations refer to this study.
[b]) From a photograph of a female carrying an oötheca
[c]) Oviposited by one female
[d]) Oviposited by 2 females
[h]) ? means that the number observed was not mentioned.
[m]) One of these females also rotated to the right.
[s]) These 2 females also rotated to the right.

The possible stages through which rotation evolved in the Blaberoidea, from a polyphagid-like form is given in Fig. 25. The examples shown are not necessarily the ancestral lines. A species in which the oötheca possessed a long flange and was not rotated could have given rise, by reduction of the flange, to a blattellid-like species that did not rotate, or to a polyphagid-like stock that had a primitive type of rotation in which none of the eggs were held within the vestibulum. The polyphagids with primitive rotation could have evolved into advanced rotating individuals, by a complete loss of the flange, thus allowing the anterior eggs in the oötheca to remain in the vestibulum of the female. However, advanced rotation also could have arisen from a non-rotating blattellid whose oötheca lacked a flange and in which the anterior eggs were already housed in the vestibulum. Longer retention of the oötheca led to species like *Blattella* and finally retraction into the uterus occurred with the final evolution of ovoviviparity, and viviparity in the Blaberidae.

Since all of the Blaberidae that have been observed ovipositing are levorotatory (i.e., they rotate the oötheca so the keel faces the left), they probably arose from a *Blattella*-like stock that was levorotatory. Table 1 shows the direction of rotation of different species of Blattellinae. With the exception of *Ectobius panzeri* and *Ischnoptera rufa rufa,* the females of most species observed are dextrorotatory (i.e., they rotate the oötheca so the keel faces the right). Thirty percent of the oöthecae of *Ischnoptera rufa rufa* were rotated to the left (Table 1). Individual oviposition records were kept of 15 females of *I. rufa rufa* (Table 2), and it was found that 4 females were levorotatory, 4 were dextrorotatory, and 7 rotated in either direction. However, females that rotated their oöthecae in both directions usually rotated predominately in one direction only (Table 2, females 5,7,8,10,11).

Because the oöthecae of *Blattella* spp. remain attached to the female during embryogenesis and the eggs gain water from the mother, this genus is considered to be an important link between the oviparous Blattellidae and the ovoviviparous and viviparous Blaberidae (Roth, 1967). However, the 4 species of *Blattella* usually rotate their oöthecae to the right (Table 1), whereas all the internal incubators (Blaberidae) are levorotatory.

Brown (1952) suggested that *Ectobius panzeri* which generally rotates its oötheca to the left (Table 1) probably tends to rotate the egg case towards the side with the most eggs (if there is an odd number of eggs produced). I counted the eggs in 20 oöthecae of *Blattella germanica,* all of which had been rotated to the right; in making the counts the terminal eggs (those laid first and last) were not included since these are placed about on the midline and each lies partly on the left and right sides. Ten of the 20 oöthecae had an even number of eggs on each side. Of the remaining 10 oöthecae, 9 had one more egg on the left side, and 1 had one more egg on the right side. These results contradict Brown's hypothesis and it is likely that the direction of rotation is not influenced by the number of eggs on either side of the oötheca.

Table 2. — Individual oviposition records of females of *Ischnoptera rufa rufa* showing the direction of rotation of their oöthecae.

Female Number	Number of Oöthecae Rotated to: Left	Right
1	6	0
2	4	0
3	2	0
4	2	0
5	4	1
6	3	4
7	2	5
8	2	5
9	2	3
10	1	5
11	1	4
12	0	5
13	0	6
14	0	7
15	0	7

All of the females of *Blattella germanica* in our culture rotate their oöthecae in one direction only, usually to the right. Although I recorded only one left-rotating female in Table 1, I have observed several others and none rotated their oöthecae in both directions. In rare cases the oötheca is carried with the keel dorsad, or the oötheca is incompletely rotated and is only slightly tilted to one side (Wheeler, 1889; Ross, 1929; Willis *et al.,* 1958). It seems logical that the direction of rotation is a genetic character and by inbreeding I have tried to obtain a strain of *Blattella germanica* in which the left rotating females occur more frequently. Initially, I reared 206 female offspring from dextrorotatory mothers. Only one of the offspring rotated to the left and the remaining 205 were dextrorotatory like their mothers. The one left-rotating female oviposited 4 times and all her oöthecae were rotated to the left. The offspring of each of these oöthecae were reared and brothers and sisters were randomly inbred. The results from the females of the four oöthecae were as follows:

Oötheca Number	*Number of Females Rotating to the:* *Left*	*Right*
1	0	10
2	1	10
3	1	14
4	0	10

The 2 left-rotating females have been inbred with their brothers but the females have not yet matured, as of this writing.

The offspring from several oöthecae of the left-rotating female shown in Table 1, were inbred and the direction of rotation of the resulting females was recorded with the following results (these females were discarded after the eggs in the first oötheca hatched):

Oötheca Number	*Number of Females Rotating to the:* *Left*	*Right*
1	0	13
2	0	11
3	1	4
5	1	9

The 13 right-rotating females from oötheca number 1 (above) were reared and the F_1 individuals were randomly mated to their brothers. Each female oviposited from 3 to 5 times, producing a total of 57 oöthecae all of which were rotated to the right. The offspring of 12 of the above F_1 females were randomly inbred to their brothers and all of 202 F_2 females that were reared rotated their oöthecae to the right.

The one levorotating female from oötheca number 3 (above) was mated to a brother and their offspring were mated to 2 different males (A and B) that originated from the same oötheca. Four of the five females mated to male A produced 3 to 4 oöthecae each (total of 13), all of which were rotated to the right. One female produced 3 oöthecae all rotated to the left. Unfortunately, this female did not mate and none of the eggs hatched. The six females mated to male B each produced 3 oöthecae (total 18) all of which were rotated to the right. The one left-rotating female from oötheca number 5 (above) has been inbred but the offspring have not yet matured. The offspring of the females mated to brothers A and B were inbred and the results of these crosses were as follows:

Female No.	Number of Female Offspring Rotating: Left	Right
Mated to ♂ A		
1	0	15
3	0	35
5	1	24
Mated to ♂ B		
6	0	18
7	1	4
8	0	8
9	0	24
10	0	17
11	2	8

These experiments are still in progress but it is clear that if rotation is a genetic trait it is probably polygenic. Many genes may be involved in determining the direction of rotation of the oötheca and a long period of intensive inbreeding may be required to show this. One difficulty lies in the fact that although one can select levorotatory females for breeding, the males have no comparable visible character to indicate what their genetic makeup is for this trait.

SUMMARY

All cockroaches extrude their eggs with the micropylar ends dorsally oriented and the keel of the oötheca facing upwards. Some species carry the oötheca in this position until depositing it, whereas others rotate the egg case 90° before dropping or retracting it into the uterus. The position in which the oötheca is carried at the time it is deposited is significant taxonomically and also played an important role in the evolution of ovoviviparity and viviparity.

Rotation occurs only in some members of the Blaberoidea (Polyphagidae, Blattellidae, and Blaberidae — the phyletic line in which internal incubation evolved) but not in the Blattoidea (Cryptocercidae and Blattidae — the line in which ovoviviparity did not evolve). Rotation reoriented the oötheca so that the long axes of the eggs lay in the plane of the cockroach's width, a position which allowed for the stretching of the uterus once the egg case was retracted into the female's body. Rotation in the oviparous Blattellidae may be considered to be a preadaptation for the evolution of internal incubation in the Blaberidae.

The type of rotation found in the Polyphagidae is considered to be primitive because none of the eggs are hidden within the vestibulum; the polyphagid oötheca has a flange by which it is held in the

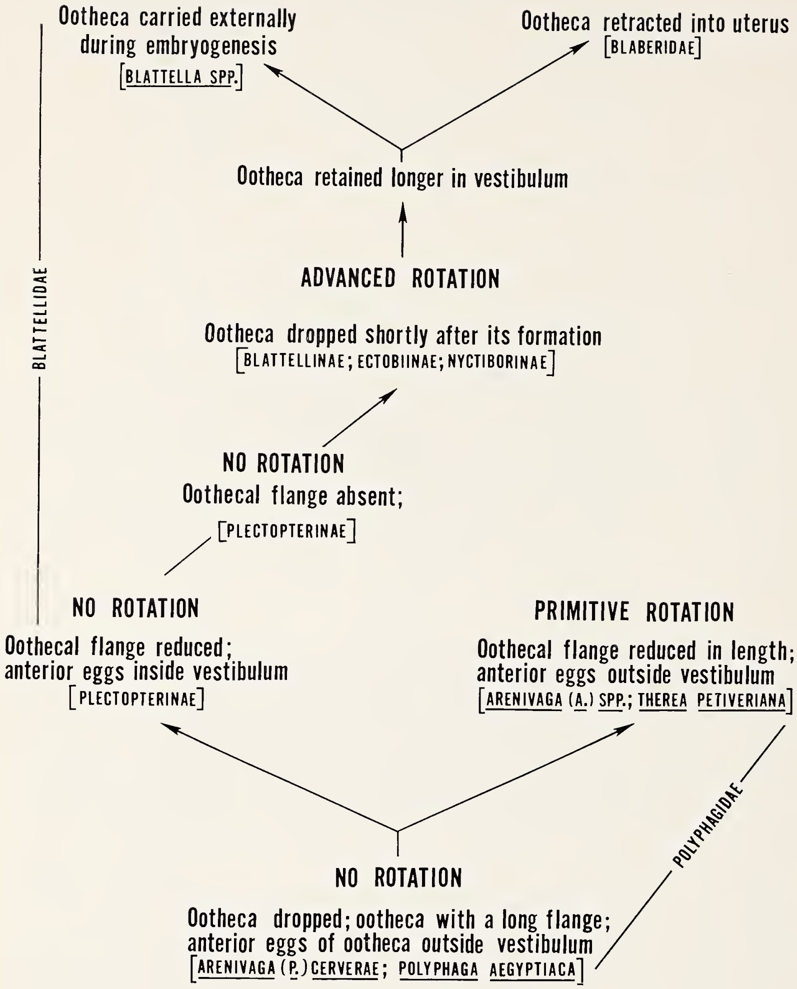
Ootheca carried externally during embryogenesis
[BLATTELLA SPP.]
Ootheca retracted into uterus
[BLABERIDAE]
Ootheca retained longer in vestibulum
ADVANCED ROTATION
Ootheca dropped shortly after its formation
[BLATTELLINAE; ECTOBIINAE; NYCTIBORINAE]
NO ROTATION
Oothecal flange absent;
[PLECTOPTERINAE]
BLATTELLIDAE
NO ROTATION
Oothecal flange reduced; anterior eggs inside vestibulum
[PLECTOPTERINAE]
PRIMITIVE ROTATION
Oothecal flange reduced in length; anterior eggs outside vestibulum
[ARENIVAGA (A.) SPP.; THEREA PETIVERIANA]
POLYPHAGIDAE
NO ROTATION
Ootheca dropped; ootheca with a long flange; anterior eggs of ootheca outside vestibulum
[ARENIVAGA (P.) CERVERAE; POLYPHAGA AEGYPTIACA]

Figure 25. Possible pathways showing how rotation of the oötheca in the Blaberoidea and subsequent retraction of the egg case into a uterus could have evolved from a polyphagid-like ancestor.

female's paraprocts. The rotation exhibited by the Blattellidae (Blattellinae, Ectobiinae, and Nyctiborinae) and all of the Blaberidae is more highly evolved or advanced because once rotated the anterior eggs in the oötheca are in close contact with the tissues in the vestibulum. This contact was essential for the evolution of ovoviviparity and viviparity, because in species like *Blattella,* the eggs, which are carried externally, obtain water from the female.

The evolution of rotation from a polyphagid-like form whose oötheca had a long flange and was not rotated, may have occurred as follows: Reduction of the flange could have resulted in a blattellid-like species that did not rotate its oötheca and a polyphagid-like stock with a primitive rotation. Advanced rotation could have evolved from a non-rotating blattellid whose oötheca had already lost the flange.

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THE LIFE-CYCLE OF THE SPIDER *PHIDIPPUS COCCINEUS* (SALTICIDAE) UNDER LABORATORY CONDITIONS*

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The jumping spider, *P. coccineus,* spends the winter in penultimate instar within a heavy hibernating web under stones. Usually, the spider undergoes its final molt just before it emerges, in April or in May, and resumes its nomadic bushtop existence. Mature males appear before the females do. In the spring of 1967, for example, twenty spiders were collected during the first week of April: seven of these were mature males, three were mature females, and the remaining ten were females in the penultimate instar that became mature between 12 April and 23 April. The earlier date of reaching maturity for males yields a chi-square of 7.9, $df = 1$, $p < .005$. Courtship and mating occur in late spring and early summer, but after mid-July adult specimens of *P. coccineus* are very difficult to find, although spiderlings of that species are abundant.

For several years, we have observed that spiders overwintering in the laboratory, with continued warmth and abundance of prey, molted abnormally early and showed a striking concordance on this anomalous date of reaching maturity. Furthermore, even though the final molt is some three months premature, the males still became mature between one and two weeks ahead of the females. The spiders that matured early also died early and, in 1967, over half were dead before spiders that had spent the winter in the field began to emerge. Table 1 presents these data for 52 spiders which spent the winter in the laboratory. These spiders came from the same population as the 20 that became mature by 23 April.

A similar phenomenon has been observed in the reproductive behavior of *Phidippus apacheanus.* Under field conditions, these spiders mate in October-November, and the gravid female spends the winter in a heavy web under stones. Although the dates for egg-laying and hatching under field conditions are not known, it seems likely that these events do not occur until spring. At any rate, spiderlings of this species first appear in June, only a few weeks before those of *P. coccineus.* Four gravid females taken to the laboratory laid their

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eggs between 12 December and 30 December; these eggs hatched in January and mobile spiderlings emerged from the nest in February. Parenthetically, two of the early maturing *P. coccineus* females were mated with early maturing males; the eggs were laid in February, and the spiderlings emerged in March.

The fact that both sexual maturity and death in *P. coccineus* were accelerated by overwintering in the laboratory implies that, like the proverbial candle that cannot burn at both ends, the life span of this spider depends more on metabolic processes than on calendar time.

By accelerating maturity with laboratory maintenance conditions, it is possible to bring together young adults of *P. coccineus* and *P. apacheanus*. Thus, the technique could provide the basis for a study on mechanisms of reproductive isolation in these two species. Normally, the adults of *apacheanus* and *coccineus* appear in the same habitat at different times of the year, so that the time at which each species is courting does not overlap (Gardner, 1965).

Finally, the fact that the spiders had been under constant conditions of warmth and abundance of prey for about three months without molting, while during July-September the intermolt interval for 25 *P. coccineus* was 27 ± 5.5 days, and that they subsequently molted within a relatively short time (for males, 3 January ± 13 days, and for females 13 January ± 11 days), suggests the following

TABLE I

Maturity and Survival of *P. coccineus* Overwintering in the Laboratory (Winter '66-'67: N - 52; 26 became adult ♂♂; 11 became adult ♀♀; 15 died before maturity.)

	Percentage of group reaching:					
	Penultimate Instar		Adult Stage*		Death**	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Before the 1st day of:						
Oct.	0	11%				
Nov.	96%	89%				
Dec.	4%		0			
Jan.			36%	0	0	0
Feb.			64%	100%	28%	11%
March					32%	22%
April					8%	22%

*The ♂♂-♀♀ difference is significant at p = 04, Fisher's exact method.

**32% of the males and 44% of the females survived beyond April 1 and were released in the field.

mechanism for controlling the final molt. Suppose that constant conditions of warmth and abundance of food produce a regular interval of four weeks between molts throughout the summer but that a hormone is activated following the penultimate instar which inhibits further molting. Gradually, this inhibitory substance wears off. Then the spider can respond to environmental conditions again and if, during a brief sampling period, it is exposed to favorable environmental conditions, it will molt. Such a mechanism could be highly adaptive as the spiders would not initiate a disastrous breeding season during an Indian Summer, and could take advantage of an early spring.

Some fragmentary evidence supports this hypothesis: occasionally, spiders have been collected in their heavy webs during the winter, and brought to the laboratory where they soon resumed feeding. Under these conditions, two penultimate males collected on 4 December became mature on 5 January and 12 January respectively. Further experiments along these lines, that is, with favorable environmental conditions administered in short samples at different times during the winter would test the suggestions on inhibition. Furthermore, the favorable conditions should be specified more closely, as Turnbull (1962, 1965) has done for the relationship between daily food consumption and development in *Linyphia triangularis* and *Agelenopsis potteri.*

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DEFENSE MECHANISMS OF ARTHROPODS. XX. QUANTITATIVE ASSESSMENT OF HYDROGEN CYANIDE PRODUCTION IN TWO SPECIES OF MILLIPEDES[1]

By H. E. Eisner, D. W. Alsop, and T. Eisner
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Although much has been learned in recent years about the chemical nature of the defensive secretions of arthropods (for reviews see Jacobson, 1966; T. Eisner and Meinwald, 1966; Roth and T. Eisner, 1962; Schildknecht et al., 1964), virtually no precise measurements have been made of the quantities in which the active principles are produced and stored. In animals that discharge their secretion as a liquid, gland capacity may be estimated directly by weighing the amount of fluid ejected. But when the defensive substance is emitted as a gas, a more refined assay is in order. In two previous papers of this series, we dealt with the production of gaseous hydrogen cyanide by certain species of millipedes, and described the structure and mode of operation of their cyanogenetic glandular apparatus (H. E. Eisner et al., 1963; T. Eisner et al., 1963). We have now developed a quick and highly sensitive assay for hydrogen cyanide, and it is our purpose here to report on the measurement of cyanogenesis in two species of millipedes, *Apheloria corrugata* and *Pseudopolydesmus serratus* (Text-fig. 1). Both are members of the order Polydesmida, the only one in which cyanogenetic species are known to occur.

Polydesmoid millipedes generate hydrogen cyanide only in response to disturbance. The poison emanates as a gas from droplets of secretion discharged by special glands that open along the sides of the body. *Apheloria* and *Pseudopolydesmus* each have a total of 22 glands, present in pairs on segments 5, 7, 9, 10, 12, 13, 15, 16, 17, 18, and 19 (Text-fig. 2). In *Apheloria,* each gland is a two-compartmented organ (Text-fig. 2). In the inner compartment (reservoir) there is stored an aqueous emulsion of mandelonitrile, the adduct of benzaldehyde and hydrogen cyanide. The other compartment (vestibule) contains a catalyst, presumably an enzyme, that promotes the dissociation of mandelonitrile. The gland is constructed

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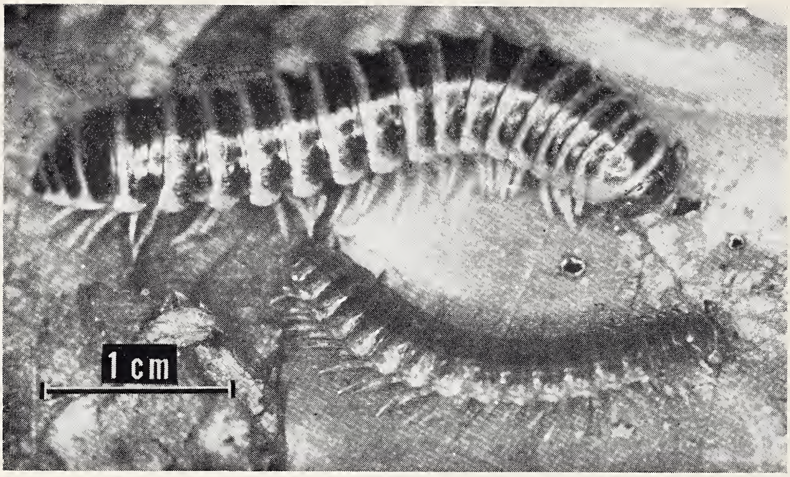
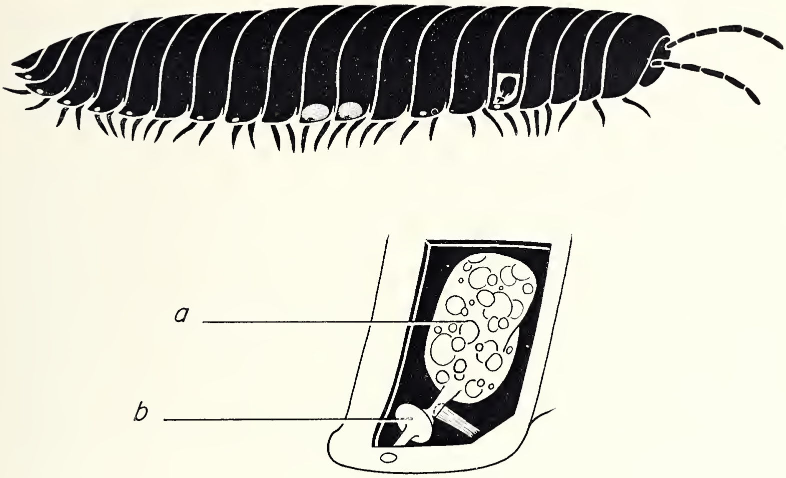


Text-fig. 1. *Apheloria corrugata* (above) and *Pseudopolydesmus serratus.*

in such a way that the contents of the two compartments are mixed, and cyanogenesis is initiated, at the instant of discharge. Cyanide liberation proceeds gradually, and persists for minutes after the discharge (H. E. Eisner et al., 1963; T. Eisner et al., 1963). The secretion and its vapors are strongly repellent to predators (T. Eisner and H. E. Eisner, 1965). *Apheloria* may discharge from one, several, or all glands, depending on the severity of the attack. A single ant, biting one of the millipede's legs, may cause only the gland nearest that leg to discharge, but this suffices to deter the assailant. A larger predator, or a swarm of ants, may inflict more generalized trauma and cause a number of glands to discharge. Ejection from all glands occurs only in response to unrestricted disturbance, such as rough handling. The preceding probably applies also to *Pseudopolydesmus,* which is known to generate hydrogen cyanide (H. E. Eisner et al., 1963), and which we have found to possess two-compartmented glands essentially similar to those of *Apheloria.* However, it is not known whether *Pseudopolydesmus* also generates hydrogen cyanide by dissociation of mandelonitrile. The fact that its secretion has an odor distinctly different from that of benzaldehyde suggests that it may store a cyanohydrin other than mandelonitrile or, alternatively, that its secretion contains additional compounds capable of masking the odor of benzaldehyde.



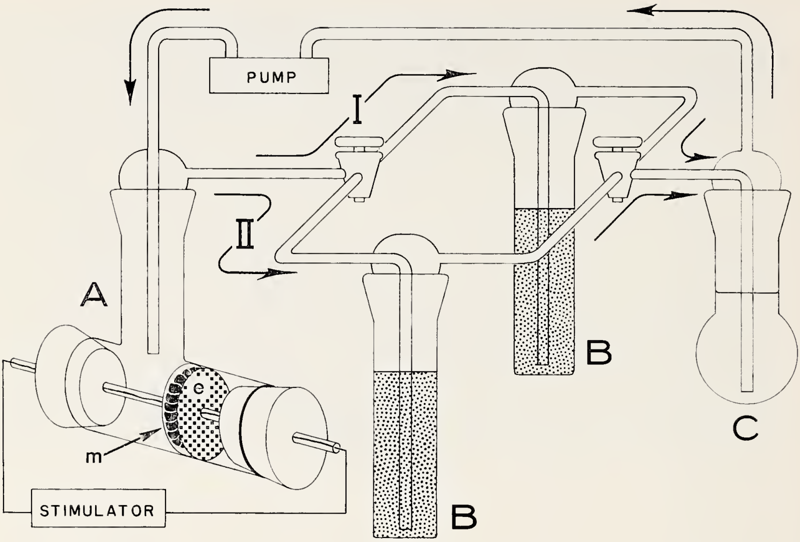
Text-fig. 2. Top, diagram of *Apheloria,* showing the gland openings (white spots) on the notal margins. Glands on segments 9 and 10 have discharged their secretion. The cutaway showing the gland in segment 5 is enlarged below. The *reservoir* of the gland (a) contains emulsified mandelonitrile. A valve operated by a muscle separates the reservoir from the smaller *vestibule* (b), which contains the catalyst.

Cyanogenesis in millipedes has never before been measured. However, naturalists have long been aware of the considerable potency of the secretion, and it had been noted that a container with cyanogenetic millipedes could serve as an effective "killing jar" in which insects and other small animals would not long survive (T. Eisner and H. E. Eisner, 1965). We have found the vapors liberated by freshly disturbed *Apheloria* to be rapidly fatal to houseflies confined with the millipede in a small vial, and others have made comparable observations (Davenport et al., 1952).

MATERIALS AND METHODS

The millipedes

Apheloria and *Pseudopolydesmus* were taken at Ithaca, N.Y., in an area of about an acre on a woody hillside beside a brook, in moist leaf litter and under rocks. They were collected at various dates throughout their active season, from early May to late November. They were assayed for hydrogen cyanide production within less than four days after capture.



Text-fig. 3. Apparatus used to stimulate millipedes electrically and to trap the hydrogen cyanide liberated. Details in text.

Special precautions were taken to prevent millipedes from discharging prematurely before the assay. When first collected in the field, they were allowed to crawl into individual vials, and from the vials into cages, without being handled in the process. Under these circumstances they do not discharge, as was determined by introducing strips of filter paper impregnated with benzidine reagent (Feigl, 1960) into the closed quarters of newly captured millipedes. The strips always remained white instead of turning blue, indicating absence of cyanogenesis. Likewise, in the laboratory, when the millipedes were transferred from cages into the apparatus used for the assay, the transfer was effected by way of vials without direct handling.

The assay

In principle, the assay for hydrogen cyanide is based on the fact (Denigès, 1895; Liebig, 1851) that a turbid colloidal suspension of silver iodide in aqueous ammonia can be converted into an optically clear solution of silver ammonium cyanide $[Ag(CN)_2NH_4]$ by addition of hydrogen cyanide (or other sources of cyanide ion). For a given volume of suspension, the amount of cyanide that causes clearness is constant, and can be determined by titration. If an unknown quantity of cyanide is added (for instance, as hydrogen cyanide from a millipede), the amount of this unknown can be calculated by titrating the remaining silver iodide to a clear end point.

Text-figure 3 shows the apparatus in which individual millipedes were electrically stimulated to discharge and the emanating vapors of hydrogen cyanide were trapped for subsequent assay. A millipede was transferred into chamber A, and the two grid electrodes (e), whose shafts fit movably through the stoppers at the ends of the chamber, were gently pressed against the animal (m) from both sides. Three electric shocks (0.5 v., 25 Hz.) of 30 sec. duration, administered at 10 min. intervals, caused the millipede to discharge its secretion[2]. A pump circulated the gas in the system directing it first through one of two alternative pathways (I, II) bearing a cyanide trap (B) with a measured amount of standardized silver iodine suspension[3], and then through a vessel (C), containing aqueous sulfuric acid, which prevented ammonia vapors, flushed from B, from reaching and harming the millipede. Since a single trap rarely sufficed to collect all the hydrogen cyanide emitted, the gas was bubbled through a series of traps. This involved routing the flow in alternate succession through I and II, and replacing the individual traps with fresh ones for as long as their tendency to clear indicated the continuance of cyanogenesis. As a rule, cyanogenesis came to a halt within 30 to 50 minutes, but in animals of high yield it often lasted beyond the hour. The final assay consisted of pooling the contents of all traps, and titrating away the residual turbidity with a standardized solution (0.01 M) of sodium cyanide. The end point of the titration was determined photometrically (Bausch & Lomb Spectronic 20 Spectrophotometer, set at $\lambda = 500$), by comparison with distilled

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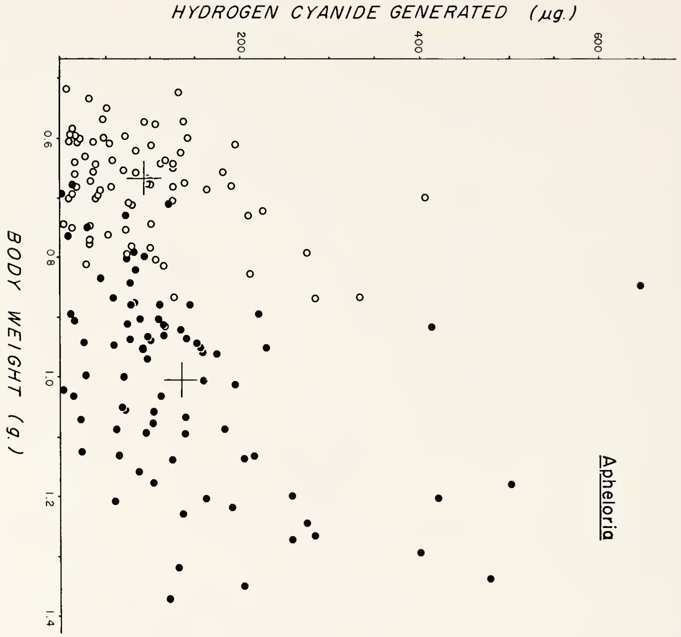
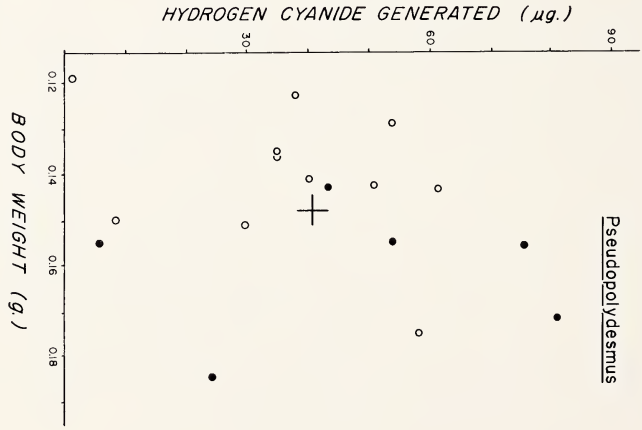
[2] This triple stimulus was adopted as a standard after it was demonstrated (by preliminary tests in which individual *Apheloria* were subjected to one or more shocks of varying intensity, frequency, and duration, and assayed for hydrogen cyanide production after each shock) that it was adequately strong to cause the animal to expel its entire secretory reserves. As a rule, the first shock sufficed to cause depletion or near depletion of the glands, which discharged visibly and usually simultaneously within seconds after onset of the stimulus. The second and third shocks evoked at most a very slight additional output of cyanide, indicating that the unexpelled residue had been minimal. Fourth shocks always proved superfluous. Specimens dissected after electric stimulation had empty glandular reservoirs. The electric shocks did not noticeably harm the millipedes, which survived as long as untreated controls (usually from two to five months).

[3] The suspension was prepared from silver nitrate (0.001M), concentrated aqueous ammonia (*ca.* 25%), potassium iodide (0.005M), and distilled water, mixed in the ratio of 10 : 2 : 1 : 87 by volume; 1 ml of this suspension is cleared by 5.4 μg hydrogen cyanide.





EISNER, ALSOP AND EISNER — DEFENSE MECHANISMS water as the standard[4]. The assay was accurate to ± 0.6 μg hydrogen cyanide, as was determined by measuring the efficiency of recovery of known amounts of hydrogen cyanide, generated in the apparatus by reaction of sodium cyanide and acid.

RESULTS AND CONCLUSIONS

A total of 157 adult *Apheloria* were tested, comprising 80 females and 77 males. Of *Pseudopolydesmus,* only 11 males and 6 females were assayed. The results, plotted as hydrogen cyanide produced against body weight of millipede, are presented separately for each species in Plate 16.

Cyanogenetic yield is evidently a markedly variable parameter in both species. *Apheloria,* which is larger than *Pseudopolydesmus,* has a higher mean yield than the latter (114 μg/animal in *Apheloria;* 41 μg/animal in *Pseudopolydesmus*). Yet *Pseudopolydesmus* has more than twice the mean output per unit body weight than does *Apheloria* (280 μg/g in *Pseudopolydesmus;* 135 μg/g in *Apheloria*).

In *Apheloria,* females tend to outproduce males; since females are also larger than males (note in Plate 16 the almost disjunct size distribution of the sexes) they probably have larger glands. Additional data might have shown the same to hold for *Pseudopolydesmus.*

Both species have considerable toxic potential, certainly at their higher levels of output. For example, a single *Apheloria,* weighing one gram and having a near maximum yield of 600 μg of hydrogen cyanide, produces the equivalent of 18 times the Lethal Dose of a 300 g pigeon, 6 times the LD of a 20 g mouse, 0.4 times the LD of a 25 g frog, and 0.01 times the LD of man (Flury and Zernik,

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[4] The shunting of the gas stream from one trap to the next sometimes occurred slightly after, rather than before actual clearness had been achieved. As a result, individual traps could contain more cyanide (as ammonium cyanide, bound to the excess ammonia in the suspension) than the predictable amount that had solubilized the silver iodide. The pooled sample was therefore sometimes clear rather than turbid. This necessitated the addition, before backtitration with sodium cyanide, of sufficient fresh suspension to bring about a reappearance of turbidity, thus insuring the conversion of all cyanide to silver ammonium cyanide. Such added suspension was tallied as part of the total in the final computation.

Explanation of Plate 16

Cyanogenetic yield of individual *Apheloria* (left) and *Pseudopolydesmus* (right), plotted against body weight (males, open circles; females, closed circles). In *Apheloria,* mean yield (horizontal bar of crosses) and mean body weight (vertical bar of crosses) differs significantly ($p<0.01$) in the two sexes. In *Pseudopolydesmus,* due to the relatively scant data, mean output and weight are given for the population as a whole (single cross).

1935; Stecher et al., 1960). For a small, appropriately sensitive predator, swallowing *Apheloria* may well have its deleterious aftereffects. However, predators do not usually consume *Apheloria,* but are repelled by the secretion and its vapors. Under such circumstances, exposure to hydrogen cyanide and systemic incorporation of the poison are likely to be minimal. It is by no means clear how hydrogen cyanide, as a dilute vapor, effects its repellent action. The possibility that it acts in conjunction (synergistic ?) with the aldehyde should not be dismissed.

The cyanogenetic capacity of a millipede can be expressed in terms of the amount of cyanohydrin stored. A medium-sized *Apheloria* (1 g) with a near maximum generating capacity of 600 μg hydrogen cyanide, has an effective defensive payload of 3.0 mg mandelonitrile, or about 0.3% of body weight. Distributed equally among the animal's 22 glands, this amounts to an individual glandular load of 0.13 mg (*ca.* 0.12 μl) or about 12% of the estimated volume (1 μl) of the reservoir of a gland. Given its emulsified state, mandelonitrile could be expected to occupy only a fraction of the total volume of the reservoir.

Attempts were made with *Apheloria* to determine the rate at which the contents of their glands are restored. Fifteen millipedes, reassayed within 8 days or less after initial depletion of their secretion, produced less than 15 μg hydrogen cyanide each. Another group of six, reassayed after 2 months, still had relatively low yield of 20 to 100 μg. Secretion is thus seen to be synthesized at a slow and somewhat variable rate.[5] Millipedes reassayed after four and five months produced little more than those reassayed after two months. However, this may reflect the fact that after two months the health of laboratory animals declined (as reflected by a sharp rise in mortality) and that their rate of secretory synthesis had become subnormal. *Pseudopolydesmus* apparently also reloads its glands slowly. When individuals that had been previously stimulated to depletion were subjected to rough handling several days later, they failed to give off the noticeable odor that is indicative of a discharge.

In view of the slow rate of synthesis of secretion, it is clear that in the four days or less that elapsed between capture and first assay the individual millipedes could not have added substantially to their secretory resources. The variability in output depicted in Plate 16 is therefore probably a fair representation of the actual variability that prevails in nature. *Apheloria* collected early in the season (first week of May) had as variable an output as those collected in midsummer or late November. In *Pseudopolydesmus,* output was also broadly variable on the two occasions that the species was collected (May and October). One wonders about the meaning of this variability. The fact that most millipedes have a yield that is considerably below the maximum recorded for their species might be taken to indicate that their glands are in a state of partial depletion and that encounters with predators are commonplace throughout the season. However, cyanogenetic potential may also be subject to instrinsic variation, and a submaximal yield need not by necessity reflect a history of past assault. Attempts to raise *Apheloria* in the laboratory in order to determine whether in the absence of predation their cyanogenetic potential achieves uniformity at high levels met with failure.

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[5] No correlation was apparent between the magnitude of the initial yield and that subsequently obtained on reassay (a high initial output was sometimes followed by a relatively slow rate of synthesis, and vice versa).

In an undisturbed millipede, there is no detectable spontaneous loss of hydrogen cyanide. Assays performed on groups of five millipedes, confined undisturbed in chamber A of the apparatus for up to two days, invariably proved negative. Thus, the valve that ordinarily seals the connection between the two compartments of each gland

Organism	Cyanogenetic Capacity µg/g
Prunus serotina (Wild black cherry)	2100
Prunus amygdalus (Bitter almonds)	1800
Triglochin sp. (Arrowgrass)	500
Bahia oppositifolia (Bahia grass)	300
Pseudopolydesmus serratus	280
Apheloria corrugata	135

Table I. Mean cyanogenetic output of *Pseudopolydesmus* and *Apheloria,* compared with some of the higher cyanogenetic capacities recorded for plants (compiled from references in Kingsbury, 1964, and Wokes and Willimott, 1951).

(text-fig. 2) and prevents the contents from interacting, must be virtually leak proof. Lack of output under these conditions also demonstrates that casual contact with other millipedes, such as occurred almost continuously during confinement in the chamber, does not constitute an appropriate stimulus for the discharge.

Cyanogenesis in animals is rare, and so far as known is restricted to polydesmoid millipedes and certain moths (Jones et al., 1962). But among plants it is widespread, and occurs in several hundred species of diverse families (Seifert, 1955). The mechanism in plants may also be defensive, since as a rule the liberation of hydrogen cyanide is initiated only in response to injury. Cyanogenetic capacity of plants has been measured, and found to vary over a broad range. Mean output in *Apheloria* and *Pseudopolydesmus* is below the upper range of values recorded from plants (Table 1). However, this comparison is of only limited significance. The values for plants are usually obtained by measuring the cyanide released after complete trituration of whole plants or parts thereof. Actual amounts liberated spontaneously by a plant for defensive purposes — as, for instance, when an insect bites into one of its leaves — has never been measured. The technique described here may be sufficiently sensitive to be employed for this purpose.

SUMMARY

1. A simple photometric assay for hydrogen cyanide is described, sensitive to 0.6 μg.

2. The assay was used to measure the cyanogenetic output of the defensive glands of two species of polydesmoid millipedes, *Apheloria corrugata* and *Pseudopolydesmus serratus.*

3. Output is highly variable in both species. Mean yield is 114 μg HCN in *Apheloria,* and 41 μg HCN in *Pseudopolydesmus.* Recorded maxima for each species are, respectively, 645 and 81 μg HCN.

4. The assay should prove useful for measuring cyanogenesis in other organisms, including plants.

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THE ELECTRENTOMOID PSOCIDS (PSOCOPTERA)[1]

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The psocids dealt with in this paper, the electrentomoids, are forms resembling amphientomids but lacking scales or at most having a vestiture of minute scale-like structures on the wings. Universally, the subcosta of the forewing describes an arc and rejoins the radius. There is a tendency, not universal, for the two anal veins of the forewing to join together before reaching the wing margin.

These psocids were first treated taxonomically by Enderlein (1911: 337) as the subfamily Electrentominae of Amphientomidae, to accommodate the single genus *Electrentomum*, with a single included species, *E. klebsianum*, from Baltic amber. A second genus, *Parelectrentomum*, with a single species, *P. priscum*, also from Baltic amber, was described by Roesler (1940:228). A third genus, *Manicapsocus*, the first living form assigned to the Electrentominae, was described by Smithers (1965:46) from Angola.

Also included among the electrentomoid psocids are *Compsocus* Banks (1930:183) and *Plaumannia* Roesler (1940:234). Banks placed *Compsocus* in the family Amphientomidae due to the presence of minute scale-like structures forming the vestiture of the surface of the forewing. The wing venation and other characters mark this genus as clearly electrentomoid. Roesler made *Plaumannia* the basis of a new family, Plaumanniidae. I retain this group as one of the electrentomoid families, but give it a new name (Troctopsocidae) because of homonymy of *Plaumannia*.

I have been able to examine specimens of all of the described living species of electrentomoids plus representatives of six new genera and fourteen new species from the American tropics. The new forms are described here and three new families are erected. *Compsocus* and *Troctopsocus* are redescribed; notes on *Manicapsocus* are included, as is a key to the genera. Finally, a preliminary attempt is made to

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assess the phylogeny of the electrentomoids. In the section on phylogeny, I discuss reasons for not regarding the electrentomoids as a single taxon at any level, although I previously considered them to form a single family (Mockford, 1966).

Measurements were taken principally from whole specimens mounted temporarily in glycerine. The degree of precision of the measurements is indicated as follows: for wing measurements the micrometer unit equals 22.2μ, for tibial measurements the micrometer unit equals 7.5μ, and for all other measurements the micrometer unit equals 3.7μ.

Terminology — The term clunium is used for the fused dorsal and lateral sclerotized regions of abdominal segments 8 through (probably) 10. The rounded cushion-like field of the paraproct generally bearing trichobothria is called the paraproctal sensorium. Both of these designations follow Pearman (in litt.). A sclerite of the subgenital plate, generally in the form of a letter T is designated T-shaped sclerite, although it may take other forms. The sac of the spermatheca is divided into two regions, one adjoining the duct, and the other further from the duct. The former is designated basal region, and the latter distal region. The lacinial tip generally has two principal tines, here called median and lateral cusps, indicating the positions which these structures usually hold in relation to the midplane of the insect, although the lacinia is capable of a certain amount of rotation. In the bilobed third ovipositor valvula, the larger, more basal lobe is designated primary lobe, and the smaller, more distal lobe is designated secondary lobe.

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Specimens for study were borrowed in part from the Illinois State Natural History Survey, (Urbana), the United States National Museum (Washington, D.C.), and Mr. C. N. Smithers (Australian Museum, Sydney). Dr. Dale E. Birkenholz of Illinois State University collected the unique type of one species in Costa Rica. Dr. W. L. Brown, Jr., of Cornell University (Ithaca, N. Y.) sent the first specimen of the bizarre form *Protroctopsocus enigmaticus* n. gen., n. sp., which aided considerably in placing this project in proper perspective. Dr. Brown's notes on the collecting site of that species were sufficiently precise so that I was able to go to the spot and collect a series of the species.

The descriptive statistics based on measurements and ratios were run on an IBM 1620 computer. The program was borrowed from Dr. R. B. Selander, University of Illinois, Urbana, and was adapted to our computer by Dr. S. K. Wong, my research associate, and Mr. Brian Crissie of the Illinois State University Computer Center.

To all of the above mentioned individuals and institutions I wish to express my sincere thanks.

CLASSIFICATION OF THE ELECTRENTOMOID PSOCOPTERA

The electrentomoids are here arranged in the following families and genera:

- Musapsocidae, new family
  - *Musapsocus,* new genus
- Troctopsocidae, new name for Plaumanniidae Roesler
  - *Protroctopsocus,* new genus
  - *Troctopsoculus,* new genus
  - *Troctopsocopsis,* new genus
  - *Troctopsocus,* new name for *Plaumannia* Roesler
- Manicapsocidae, new family
  - *Manicapsocus* Smithers
  - *Epitroctes,* new genus
- Compsocidae, new family
  - *Compsocus* Banks
  - *Electrentomopsis,* new genus
- Genera Incertae Sedis (probably Manicapsocidae or Compsocidae)
  - *Electrentomum* Enderlein
  - *Parelectrentomum* Roesler

ARTIFICIAL KEY TO THE GENERA OF ELECTRENTOMOID PSOCOPTERA

1a. Vein M in hindwing simple .... 3.

1b. Vein M in hindwing branched .... 2.

2a. First segment of Rs in hindwing present. Forewing membrane covered with tiny scale-like structures .... *Compsocus* Banks (*C. elegans* Banks).

2b. First segment of Rs in hindwing absent. Micro-vestiture of forewing membrane in form of short points .... *Electrentomopsis*, n. gen. (*E. variegatus*, n. sp.).

3a. Pterostigma closed basally .... 4.

3b. Pterostigma open basally .... 8.

4a. Cubital loop joined to M_3 by a crossvein .... *Protroctopsocus*, n. gen. (*P. enigmaticus*, n. sp.)

4b. Cubital loop not joined to M .... 5.

5a. First segment of Rs in hindwing present .... *Parelectrentomum* Roesler (*P. priscum* Roesler, Oligocene, Baltic amber).

5b. First segment of Rs in hindwing absent .... 6.

6a. With 15 antennal segments .... 7.

6b. With 13 antennal segments .... *Electrentomum* Enderlein (*E. klebsianum* Enderlein, Oligocene, Baltic amber).

7a. Vein 2A of forewing not joining 1A; R_1 in forewing widened to form a dark spot in region of its junction with wing margin .... *Manicapsocus* Smithers (*M. alettae* Smithers, Rhodesia).

7b. Vein 2A in forewing joining 1A; R_1 normal .... *Epitroctes*, n. gen. (*E. tuxtlarum*, n. sp.).

8a. Cubital loop joined to M_3 .... *Troctopsocus* (new name for *Plaumannia* Roesler).

8b. Cubital loop not joined to M_3 .... 9.

9a. Two claws of each pretarsus alike, each with two preapical teeth .... *Troctopsoculus*, n. gen. (*T. morenus*, n. sp.).

9b. Two claws of each pretarsus unlike: anterior claw (of each pretarsus) bearing membranous cowl-like swelling enclosing all but tip of claw shaft .... 10.

10a. Pterostigma broader than preceding cell. Wings unmarked .... *Musapsocus*, n. gen.

10b. Pterostigma narrower than preceding cell. Forewing marked with a vague pattern .... *Troctopsocopsis*, n. gen.

Family **Musapsocidae,** new family

Diagnosis. — Antennae of 12 segments. Frontal sutures absent. Lacinial tip with three tines composed of the median cusp, the tip of the lateral cusp, and a subapical denticle of the lateral cusp. Tarsi two-segmented. Pretarsal claws of each foot unlike, the anterior claw broadened by a membranous covering or cowl, the posterior claw without a cowl and bearing a preapical denticle. Pterostigma open basally. Vein 2A of forewing joining 1A or ending freely without joining wing margin. First segment of Rs in hindwing absent, but two ends of the vein sometimes present. Third ovipositor valvula not bilobed apically.

Genus **Musapsocus,** new genus

Diagnosis. — With the characters of the family.

Type species: *M. huastecanus,* new species

Musapsocus huastecanus, new species

Diagnosis. — Vein 2A in forewing ending freely, joining neither 1A nor wing margin. Male with three pairs of papillar fields on dorsum of clunium, the most posterior pair narrowly separated on midline and reaching posterior clunial margin; small median papillar field present on dorsum of eighth abdominal segment. Male with parameres joined to form slender rod anteriorly. Female with first ovipositor valvula bearing a short rounded lobe on mesal margin near base; third valvula with no indication of bilobing. Female subgenital plate with posterior margin flat; plate lacking T-shaped sclerite.

Male. — Measurements (Table I).

Morphology. — Lacinial tip (fig. 6): median cusp showing line through tip suggesting it to be slightly bifid. Hypandrium with posterior margin thickened and curved. Phallosome (fig. 7): parameres with basal line of fusion extending nearly to extreme base; posterior branching of parameres resulting in (1) pair of short,

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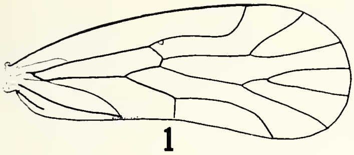
EXPLANATION OF PLATE 17

Fig. 1. — *Musapsocus creole,* n. sp., ♀, forewing.
Fig. 2. — *M. creole,* n. sp., ♀, hindwing.
Fig. 3. — *M. creole,* n. sp., ♀, lacinial tip.
Fig. 4. — *M. creole,* n. sp., ♂, phallosome.
Fig. 5. — *M. creole,* n. sp., ♀, pretarsal claws.
Fig. 6. — *M. huastecanus,* n. sp., ♂, lacinial tip.
Fig. 7. — *M. huastecanus,* n. sp., ♂, phallosome.
Fig. 8. — *M. tabascensis,* n. sp., ♀, lacinial tip.
Fig. 9. — *M. tabascensis,* n. sp., ♂, phallosome.
Fig. 10. — *M. birkenholzi,* n. sp., ♂, forewing.
Fig. 11. — *M. birkenholzi,* n. sp., ♂, phallosome.



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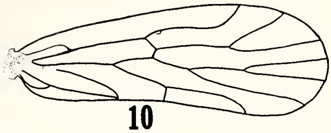

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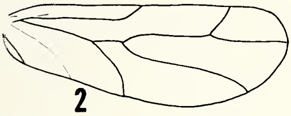

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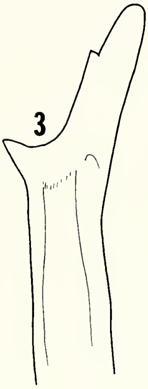

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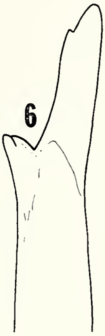

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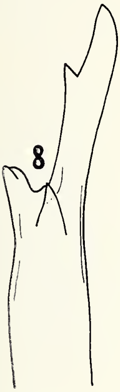

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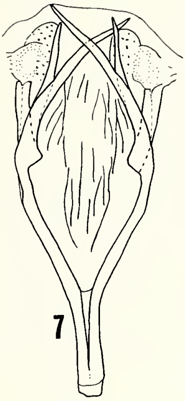

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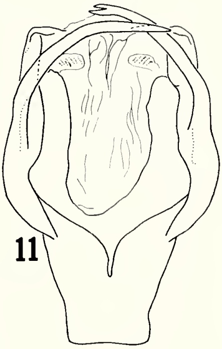

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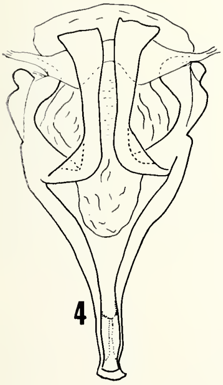

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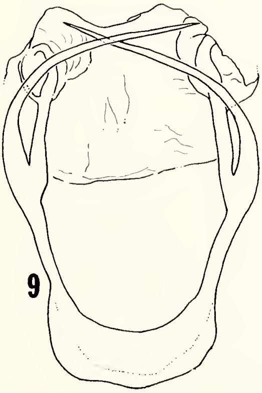

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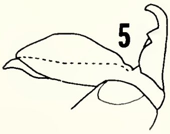

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MOCKFORD — ELECTRENTOMOID PSOCIDS

straight lateral arms each of which apparently re-divides, the resulting two rods running closely parallel and terminating in sac-like structure; (2) pair of long median arms, each of which re-divides near its base, the median sub-branches of the two sides curving toward midline and crossing near their tips; lateral sub-branches each surrounded nearly to tip by thin-walled sac containing granules. Anterior and posterior margins of clunium thickened. Clunial papillar fields (fig. 12) distributed as follows: two transverse lateral fields at about one-third distance from anterior to posterior margin; two rounded lateral fields at about two-thirds distance from anterior to posterior margin; a transverse field along posterior margin with slight median interruption. A small papillar field on pre-clunial tergum. Paraproctal sensorium with 9-10 trichobothria and 1-2 setae without basal rosettes.

Color (in alcohol). — Body and appendages largely dull ivory yellow. Compound eyes black. Reddish brown pigment distributed as follows: inner rims of lateral ocelli and upper rim of median ocellus, a small circle antero-ventral to each antennal base, a spot between compound eye and antennal base, a line along suture between ante- and post-clypeus but absent from broad central region, an irregular spot above each subgenal suture, a broad band along each side of thorax, an arc around pleural border of each coxa, an irregular band along each side of abdomen from base to clunium, the bands of the two sides connected by transverse dorsal bands in segments 3, 4, and 5, and by broken transverse bands in segments 6 and 7; papillar fields of clunium, posterior edge of epiproct, and ventral edges of paraprocts with same pigmentation.

Female. — Measurements (Table I).

Morphology. — Subgenital plate (fig. 14) with posterior margin approximately straight and beset with 11-12 strong setae. T-shaped sclerite and interior plate absent. Ovipositor valvulae (fig. 13): first valvula with broad, rounded basal appendage; third valvula very slightly bilobed apically. Paraproctal sensorium with 8-10 long trichobothria and 2 long setae lacking or with weakly developed basal rosettes.

Color (in alcohol). — Same as in male.

Type locality. — La Union near Villa Juarez, Puebla, Mexico, November 3, 1963, E. L. Mockford collector. Holotype ♂, allotype ♀, 11 ♂ and 12 ♀ paratypes and 7 nymphs. Types are for the present in the author's collection.

Records. — Mexico: Veracruz: about 10 miles east of Orizaba on Highway 150.

Habitat. — At both localities, this species was found in dried banana leaves hanging from the tree.

Musapsocus creole, new species

Diagnosis. — Vein 2A in forewing ending freely, joining neither 1A nor wing margin. Male with continuous band of papillae across dorsum of clunium. Male with parameres joined anteriorly to form short slender rod. Female third ovipositor valvula with slight indication of bilobing at apex. Female subgenital plate with posterior margin in form of flat arc; plate bearing small T-shaped sclerite without arms.

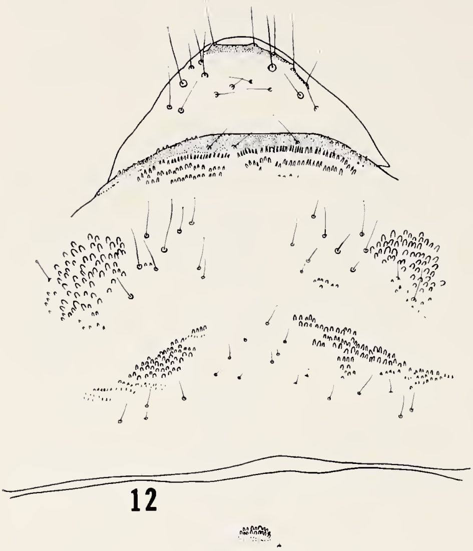
Male. — Measurements (Table I).

Morphology. — Lacinial tip (fig. 3) with median cusp simple. Hypandrium with posterior margin thickened and slightly bilobed. Phallosome (fig. 4): parameres showing basal line of fusion; posterior branching of parameres resulting in pair of converging arms curving posteriorly before meeting and having broad, truncated ends with tiny denticles on lateral margins; lateral branches of parameres curved out then in, apparently rebranching near tips. Clunium dorsally with transverse field of small denticles in anterior half, and transverse region of larger denticles (fig. 15) in posterior half. Paraproctal sensorium with 10 trichobothria and 3 setae without basal rosettes.

Color (in alcohol). — Body and appendages generally dull ivory yellow. Compound eyes black. Reddish brown pigment distributed as follows: a small circle ventro-mesal to each antennal base; diffuse granules above subgenal suture and concentrated around anterior mandibular articulation, a lateral stripe running entire length of thorax, a band across anterior border of mesonotal lobes, irregular lateral blotches on base of abdomen, a band across abdominal dorsum in region of fourth segment, a spot around each antero-lateral angle of clunium, granules irregularly distributed in epiproct and paraprocts.

Female. — Measurements (Table I).

Morphology. — Subgenital plate (fig. 22) with posterior margin slightly curved and beset with 9 stout setae. T-shaped sclerite present in form of rod with slightly thickened base. Partially cleft interior plate clearly seen through subgenital plate in preparation. Ovipositor valvulae (fig. 16): first valvula lacking basal appendage; third valvula slightly bilobed at apex. Spermatheca with sac dis-



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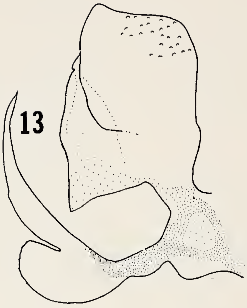

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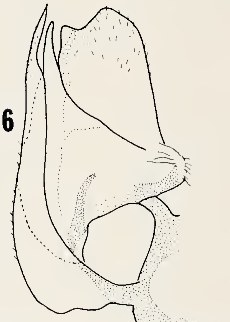

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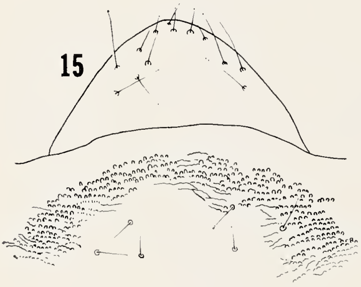

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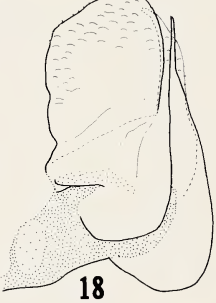

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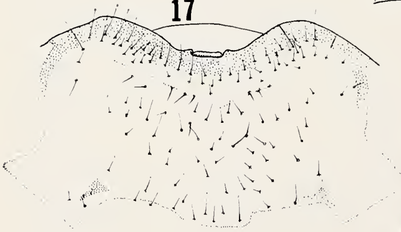

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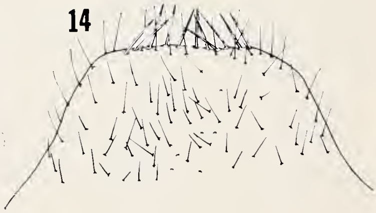

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Mockford — Electrentomoid psocids

tinctly constricted in middle forming two regions. Paraproctal sensorium with 8-9 long setae.

Color (in alcohol). — Same as in male.

Variation. — One individual was found with ocelli narrowly rimmed with reddish brown — the laterals on mesal margins, and the median on dorsal margin.

Type locality. — Rancho Grande National Park, Venezuela (elevation 1100 m.), March 5-8, 1959, E. L. Mockford and C. J. Rosales collectors. Holotype, ♂, allotype ♀, 7 ♂ and 10 ♀ paratypes and 2 nymphs. The holotype, allotype, and some paratypes will be deposited in the American Museum of Natural History (New York City); remaining paratypes will be retained in the author's collection.

Habitat. — This insect was taken from dried leaves of *Heliconia* in upland rain forest.

Musapsocus tabascensis, new species

Diagnosis. — Vein 2A in forewing generally joining 1A, at least on one side. Male with pair of papillar fields dorsally on clunium, widely separated and bordering posterior clunial margin. Phallosome with broad, rounded base. Female subgenital plate with posterior margin vaguely trilobed; plate bearing T-shaped sclerite with short arms. Third ovipositor valvula with no trace of bilobing.

Male. — Measurements (Table I).

Morphology. — Hypandrium with posterior margin thickened and bilobed; short central region reinforced by a ridge. Phallosome (fig. 9) with base broad and rounded; posterior branching of parameres resulting in median pair of straight rods, each ending in saclike region, and lateral pair of rods curved out then toward midline and crossing before their apices. Clunium with anterior and posterior margins thickened; two lateral papillar fields (fig. 23) bordering posterior margin. Paraproctal sensorium with 9 true trichobothria and a seta without basal rosette.

Color (in alcohol). — Body and legs generally dull ivory; head with slight grayish brown wash. Antennae medium brown. Com-

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Explanation of Plate 18

Fig. 12. — *Musapsocus huastecanus,* n. sp., ♂, clunial dorsum and epiproct.
Fig. 13. — *M. huastecanus,* n. sp., ♀, ovipositor valvulae.
Fig. 14. — *M. huastecanus,* n. sp., ♀, subgenital plate.
Fig. 15. — *M. creole,* n. sp., ♂, clunial dorsum and epiproct.
Fig. 16. — *M. creole,* n. sp., ♀, ovipositor valvulae.
Fig. 17. — *M. tabascensis,* n. sp., ♂, hypandrium.
Fig. 18. — *M. tabascensis,* n. sp., ♀, ovipositor valvulae.

pound eyes black. Reddish brown pigment distributed as follows: median rims of lateral ocelli and dorsal rim of median ocellus, discontinuously along suture between post- and ante-clypeus, faint irregular band along each side of thorax, pleuro-coxal border of metathorax and epimero-coxal borders of pro- and mesothoraces; narrow band across base of abdomen dorsally; complete bands across abdominal terga 3 and 4 and a pair of lateral spots in each of terga 2, 5, 6, and 7; postero-lateral borders of epiproct. Clunium pale grayish brown.

Female. — Measurements (Table I).

Morphology. — Lacinial tip (fig. 8): apex of lateral cusp pointed; median cusp slightly bifid at apex. Subgenital plate (fig. 25) with posterior margin faintly trilobed, beset with 12 strong setae; T-shaped sclerite present as a rod; small pigmented region interiorly near base of plate. Ovipositor valvulae (fig. 18): first valvula lacking basal appendage; third valvula with no trace of bilobing. Spermatheca (fig. 24): sac with constriction in about middle. Paraproctal sensorium with 10-11 typical trichobothria and one seta with poorly developed basal rosette.

Color (in alcohol). — Same as in male.

Type locality. — Palenque Ruins, Chiapas, Mexico, July 5, 1966, E. L. Mockford collector. Holotype ♂, allotype ♀, 1 ♂ and 1 ♀ paratypes. Types are in the author's collection.

Records. — Mexico: Chiapas: Finca Monte Libano in Ocosingo Valley. Tabasco: 6 miles west of Macuspana.

Habitat. — Specimens from the type locality were beaten from dried *Heliconia* leaves. The single specimen from the Tabasco locality was beaten from palm foliage.

Musapsocus birkenholzi, new species (♂)

Diagnosis. — Both forewings of single specimen with 2A joining 1A, but in right wing 2A forking just before junction, sending short vein almost to wing margin. Male with four papillar fields dorsally on clunium: one on midline at posterior margin, one on midline about half distance from anterior to posterior margin, and a pair very widely separated near anterior margin. Parameres joined anteriorly to form broad basal region of phallosome.

Male. — Measurements (Table I).

Morphology. — Hypandrium with posterior margin thickened and deeply bilobed, apparently reinforced in middle by short ridge. Phallosome (fig. 11): parameres broadened toward base with broad fused region showing partial fusion line; posterior branching of parameres resulting in pair of median, straight arms each terminating in sac-like region and pair of lateral arms strongly curving out then toward midline where tips cross; each arm bifid near its tip. Clunium (fig. 19) with margins only slightly and irregularly thickened; two lateral fields of small papillae near anterior clunial margin; compact, round field of large papillae in middle, and compact field on posterior margin along midline. Paraproctal sensorium with 6-7 trichobothria and one seta without basal rosette located centrally in field.

Color (in alcohol). — Head and antennae straw brown; thorax and legs dull ivory yellow; abdomen dull white except clunium straw brown. Compound eyes black. Reddish brown pigment distributed as follows: median rims of lateral ocelli and dorsal rim of median ocellus, irregular pale blotches on sides of thorax, a transverse band on each of preclunial terga 2 to 7.

Type locality. — Cartago, 5 Km. southeast of Turialba, Costa Rica, August 24, 1963, D. E. Birkenholz collector. Holotype ♂. The type is in the author's collection.

Musapsocus simlae, new species (♀)

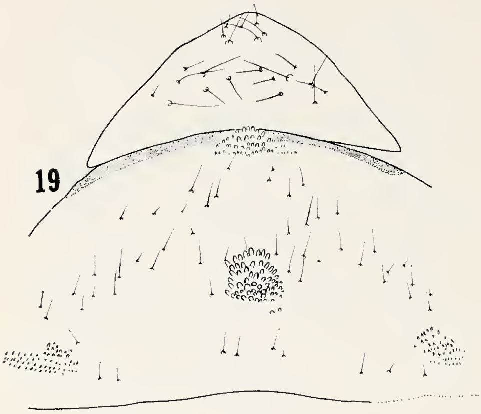
Diagnosis. — Both forewings of single specimen with 2A joining 1A. First ovipositor valvula bearing a rounded appendage at its base; third valvula with no trace of bilobing. Subgenital plate lacking T-shaped sclerite.

Female. — Measurements (Table 1).

Morphology. — Subgenital plate (fig. 21) with posterior margin deeply bilobed, bearing 13 strong setae; cleft interior plate present. Ovipositor valvulae (fig. 20): first valvula with basal appendages abutting on sclerite of spermathecal opening; second and third valvulae clearly fused for most of their length; third valvula rounded apically. Paraproctal sensorium with 10 trichobothria and a seta without basal rosette.

Color (in alcohol). — Head, thorax, and appendages generally dull ivory yellow. Abdomen dull white. Compound eyes black. Reddish brown pigment distributed as follows: scattered granules on genae and thoracic pleura, a diffuse spot on each side of each preclunial abdominal segment, a narrow band dorsally across base of abdomen, a broad diffuse band across fourth abdominal tergum.

Type locality. — Simla near Arima, Trinidad, W.I., August 30, 1961, E. L. Mockford collector. Holotype ♀. The type is in the author's collection.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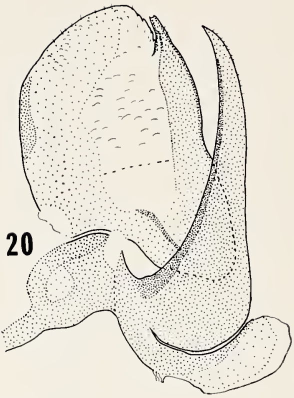
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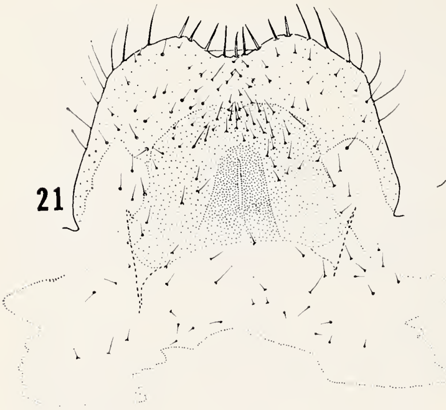
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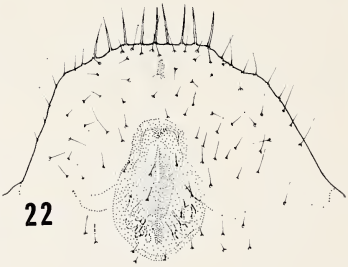
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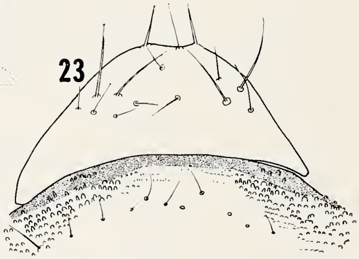
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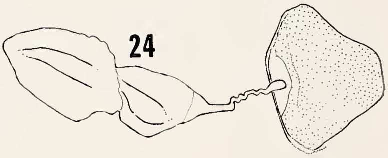
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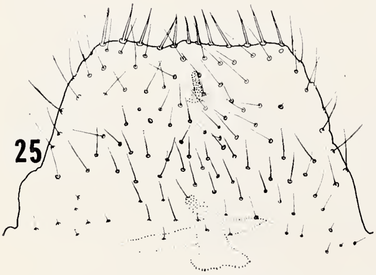
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Mockford — Electrentomoid psocids

Habitat. — The single specimen was beaten from dried leaves of *Heliconia* in upland rain forest.

Family **Troctopsocidae,** new name

Plaumanniidae Roesler, 1940, *nec* Lundblad, 1936.

Diagnosis. — Antennae of 11, 13, or 15 segments. Frontal sutures absent. Lacinial tip with medium cusp divided, lateral cusp with two or more prominent preapical denticles. Tarsi three-segmented. Pterostigma open or closed basally. Vein 2A in forewing running from its origin a short distance along wing margin, then joining 1A. First segment of Rs in hindwing present or absent. Third ovipositor valvula bilobed apically.

Genus **Protroctopsocus,** new genus

Diagnosis. — Antennae of 15 segments. Pterostigma closed basally. First segment of Rs present in hindwing. Adults (♀) occurring in macropterous and 'brachypterous' forms, the latter with forewings not much shortened, but elytriform. Macropterous form with ocelli normal, these poorly developed in brachypterous form. Frons longer than postclypeus in anterior view. Pretarsal claw with 2 preapical teeth. Terminal segment of maxillary palpus slightly swollen near tip (fig. 46).

Type species. — *P. enigmaticus,* new species.

Protroctopsocus enigmaticus, new species (♀)

Macropterous Female. — Measurements (Table I).

Morphology. — Tip of galea sculptured with reticulate pattern apparently formed by end views of closely packed column-shaped structures. Lacinial tip (fig. 28) with median cusp bidenticulate, having a small inner denticle and larger outer denticle; lateral cusp with apex apparently undivided; 3 denticles before apex, 2 more basal ones arising about at same level, much smaller than more distal one. Row of 7 spines on anterior carina of first femur. Subgenital plate (fig. 37) with apex thickened, this portion bearing 4 stout

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Explanation of Plate 19

Fig. 19. — *Musapsocus birkenholzi,* n. sp., ♂, clunial dorsum and epiproct.
Fig. 20. — *M. simlae,* n. sp., ♀, ovipositor valvulae.
Fig. 21. — *M. simlae,* n. sp., ♀, subgenital plate.
Fig. 22. — *M. creole,* n. sp., ♀, subgenital plate.
Fig. 23. — *M. tabascensis,* n. sp., ♂, clunial dorsum and epiproct.
Fig. 24. — *M. tabascensis,* n. sp., ♀, spermatheca.
Fig. 25. — *M. tabascensis,* n. sp., ♀, subgenital plate.

setae. Ovipositor valvulae (fig. 31): second valvula (not first) intimately associated at base with sclerite of spermathecal orifice; third valvula with secondary lobe very large, exceeding tip of primary lobe. Spermathecal sac with distal region larger than basal region; the duct not coiled (fig. 30). Paraproctal sensorium bearing 5 setae with poorly developed basal rosettes and 2 without basal rosettes.

Color (in alcohol). — Head pale straw brown marked with somewhat darker brown as follows: central and two lateral bands through vertex converging above ocelli; group of spots bordering compound eye mesally, largest extending almost to lateral ocellus; pair of dark reddish brown spots below ocelli; 2 or 3 dark reddish brown spots on each gena below compound eye; epistomal suture brown-bordered; postclypeus mottled with brown antero-medially. Antennae medium brown. Compound eyes black. Thorax and legs generally medium brown, the terga mottled with paler brown. Abdomen with sclerotized band of medium brown surrounding base except for two lateral breaks; remainder pale gray dorsally in preclunial segments, colorless in cuticle ventrally. Subgenital plate, clunium, epiproct, and paraproct medium brown. Forewing (fig. 26) marked with band along margin from cell R_5 through distal end of areola postica, the band including three rounded colorless spots bordering margin, one in each median cell; this band continuous with transverse one from distal end of areola postica anteriorly through distal end of pterostigma; another transverse band from fork of radial stem through nodulus; a brown spot at end of vein R_{2+3}, another at end of vein R_{4+5}, another bordering vein Cu_1a, another bordering vein 2A at base; remainder of wing colorless. Hindwing colorless.

Brachypterous Female. — Measurements (Table I).

Morphology. — Differing from macropterous form chiefly as mentioned in generic description. Heavy veins of forewing marking out depressed cells. Hindwings very short, in length equalling about width of thorax, held away from body, their tips nearly contacting inner surfaces of forewings; their venation greatly reduced.

Color (in alcohol). — Essentially same as in macropterous form.

Type locality. — Cuesta de Chipinque near Monterrey, N.L., Mexico, (elevation about 1360 m), July 16-18, 1965, collected by Cornell University Mexico Field Party. Same locality, December 28, 1965 and June 11, 1966, E. L. Mockford collector. Holotype macropterous ♀, 2 macropterous ♀ paratypes, 22 brachypterous ♀ paratypes, and 9 nymphs. The types are at present in the author's collection.

Habitat. — This species occurs in dried leaf litter in the mouths of small caves and other sheltered depressions.

Genus **Troctopsoculus,** new genus

Diagnosis. — Antennae of 11 segments. Pterostigma open basally. First segment of Rs in hindwing absent. Frontal sutures present but faint. Frons longer than postclypeus in anterior view of head. Pretarsal claw with 2 preapical teeth. Terminal segment of maxillary palpus shaped as in fig. 47.

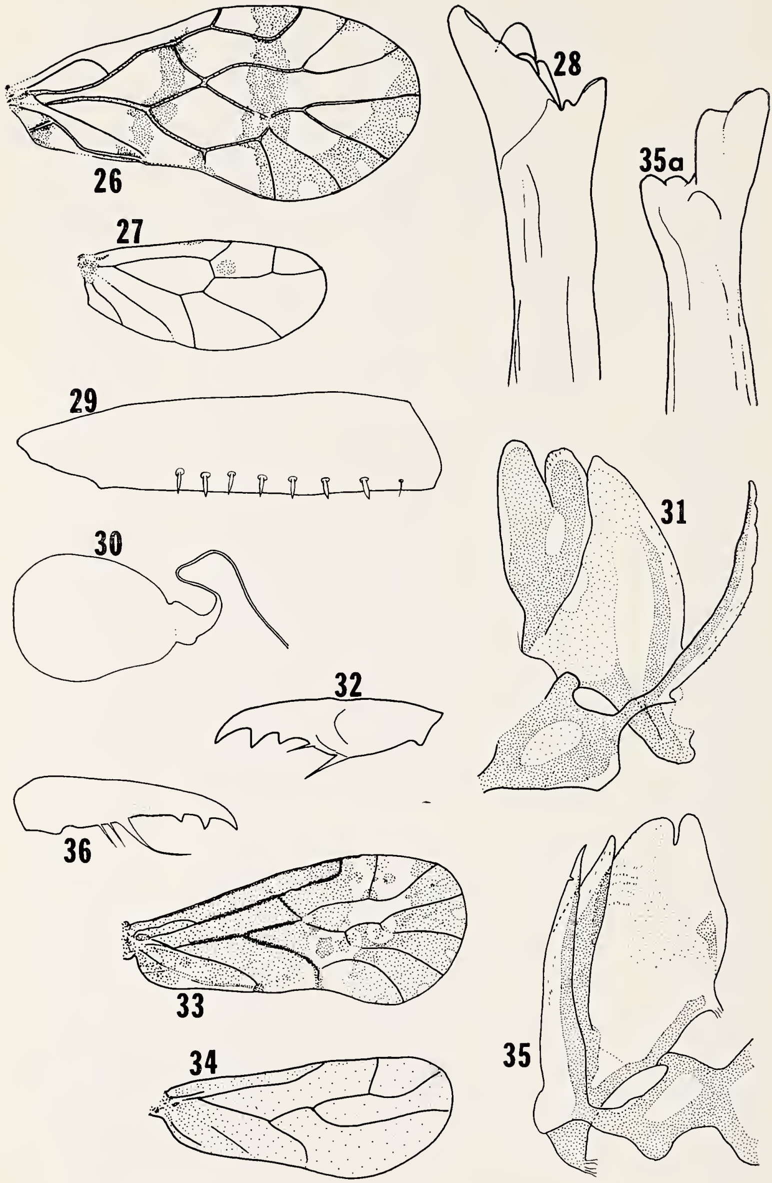
Type species. — *T. morenus,* new species.

Troctopsoculus morenus, new species (♀)

Female. — Measurements (Table I).

Morphology. — Sculpture of integument over entire frontal aspect of head: rough points densely set. Lacinial tip (fig. 35a) with median cusp bidenticulate; lateral cusp with tip divided, 2 denticles arising at about same level below tip; a low, rounded denticle arising at base of lateral cusp. Tips of galeae sculptured with reticulate pattern. Subgenital plate (fig. 38) rounded posteriorly, without stout marginal setae; stem of T-shaped sclerite with pair of lateral projections near its base. Ovipositor valvulae (fig. 35) with close connection between shafts of first and second valvulae and sclerite of spermathecal orifice; third valvula only shallowly bilobed at apex. Spermatheca with wide, curved duct; region of its orifice staining deeply in preparation; sclerite of spermathecal orifice with peripheral ring. Paraproctal sensorium with 7-8 trichobothria and 2-3 setae without basal rosettes.

Color (in alcohol). — Generally dusky brown. Vertex marked with five longitudinal lines of dark brown on paler brown background. Compound eyes dark gray. Frons dusky brown with darker longitudinal line through middle and darker mottling anteriorly. Clypeus, labrum, thoracic sclerites and legs dusky brown. Abdomen ventrally dusky brown with admixture of red except on subgenital plate. Abdomen dorsally mottled with dusky purple on background of pale underlying tissues, except clunium and telson lobes dusky brown. Forewings (fig. 33) dusky brown with irregularly-outlined clear band running diagonally across from region including vein R_{2+3} to region including base of areola postica. Pterostigma with clear spot in its middle. Each of cells R_5, M_1, M_2, M_3, and Cu_1a with clear spot bordering margin, in middle of cell except in Cu_1a where more distally placed. Cell Cu_2 clear except for two



Mockford — Electrentomoid psocids

brown spots near base and near apex. Cell 1A partially clear; cell 2A with brown basal spot but mostly clear. Hindwing with costal cell mostly cloudy brown; cloudy brown mark around apex of vein R_4+5, extending down to M and faintly beyond; faint cloudy brown wash in bases of cubital and anal cells; remainder of membrane clear.

Type locality. — 6 miles west of Macuspana, Tabasco, Mexico, April 3, 1964, E. L. Mockford collector. Holotype ♀ and 4 nymphs. The type is in the author's collection.

Habitat. — The specimens were beaten from low foliage of broad-leaved trees and shrubs in lowland rain forest.

Genus **Troctopsocopsis,** new genus

Diagnosis.— Antennae of 13 segments. Pterostigma open basally. First segment of Rs in hindwing present. Frontal sutures absent. Frons longer than postclypeus in anterior view of head. Anterior claw of each pretarsus untoothed and bearing a cowl covered with setae; posterior claw without cowl, untoothed, and bearing a long basal seta bent at its apex. Terminal segment of maxillary palpus shaped as in figure 48. Subgenital plate (fig. 54) with posterior margin rounded, bearing 4 stout setae in middle; plate lacking T-shaped sclerite. Phallosome a simple Y-shaped structure (fig. 44). Clunium bearing a posterior comb.

Type species. — *T. martinicus,* new species.

Troctopsocopsis martinicus, new species

Diagnosis.— Abdomen reddish brown dorsally on pre-clunial segments, darkest anteriorly and fading posteriorly; ventral surface colorless except for scattered reddish brown pigment at extreme base. Male with uninterrupted comb of posterior clunial margin

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EXPLANATION OF PLATE 20

Fig. 26. — *Protroctopsocus enigmaticus,* n. sp., ♀, forewing.
Fig. 27. — *P. enigmaticus,* n. sp., ♀, hindwing.
Fig. 28. — *P. en gmaticus,* n. sp., ♀, lacinial tip.
Fig. 29. — *P. enigmaticus,* n. sp., ♀, anterior femur,
Fig. 30. — *P. enigmaticus,* n. sp., ♀, spermatheca.
Fig. 31. — *P. enigmaticus,* n. sp., ♀, ovipositor valvulae.
Fig. 32. — *P. enigmaticus,* n. sp., ♀, pretarsal claw.
Fig. 33. — *Troctopsoculus morenus,* n. sp., ♀, forewing.
Fig. 34. — *T. morenus,* n. sp., ♀, hindwing.
Fig. 35. — *T. morenus,* n. sp., ♀, ovipositor valvulae.
Fig. 35A. — *T. morenus,* n. sp., ♀, lacinial claw.
Fig. 36. — *T. morenus,* n. sp., ♀, pretarsal claw.

bearing several short lateral teeth. Sclerite of spermathecal opening with complete peripheral ring.

Male. — Measurements (Table I).

Morphology. — Lacinial tip (fig. 53): two denticles arising toward tip of lateral cusp, both appressed to cusp; a rounded denticle on base of lateral cusp. Hypandrium with distal margin curved, slightly depressed in middle. Phallosome typical of the genus. Clunial comb (fig. 41) as described in diagnosis. Paraproctal sensorium with field of 7 trichobothria and 2 setae without basal rosettes.

Color (in alcohol). — Except for abdomen, almost exactly as described for *T. intermedius*, the chief differences as follows: brown border of epicranial suture not continuing beyond suture; brown regions bordering compound eyes on median sides very pale; medium brown spot or pair of spots below ocelli; epistomal suture bordered in reddish brown; brown lateral band of thorax extending through metathorax, almost completely reddish brown in prothorax and with much reddish brown in metathorax. Wing markings same as described for *T. intermedius.*

Female. — Measurements (Table I).

Morphology. — Subgenital plate typical of the genus. Ovipositor valvulae as described and figured for *T. luciensis.* Sclerite of spermathecal opening (fig. 52) as described in diagnosis. Paraproctal sensorium as in male.

Color (in alcohol). — Same as in male.

Type locality. — Ajoupa-Bouillon, Martinique, F.W.I., August 21, 1961, E. L. Mockford collector. Holotype ♂, allotype ♀, 28 ♂ and 13 ♀ paratypes and 13 nymphs. Types are for the present in the author's collection.

Habitat. — The type series was taken from dead fern leaves on the edge of a road-cut in an upland situation.

Troctopsocopsis intermedius, new species

Diagnosis. — Entire anterior half of abdomen reddish brown, the pigment extending further posteriorly in dorsal than in ventral region. Male with comb of posterior clunial margin interrupted in middle. Sclerite of spermathecal opening with incomplete peripheral ring.

Male. — Measurements (Table I).

Morphology. — Lacinial tip: lateral cusp with one denticle arising abruptly from cusp, another appressed to cusp; a third, rounded denticle at base of cusp. Hypandrium with distal margin curved, slightly depressed in middle. Phallosome typical of the genus.

Clunial comb (fig. 42) as described in diagnosis. Paraproctal sensorium with 7 trichobothria and a seta without basal rosette.

Color (in alcohol). — Head, thorax, and legs largely dull yellowish ivory with darker markings as follows: a medium brown stripe bordering epicranial suture and continuing through frons and postclypeus; a medium brown median border of each compound eye; a reddish brown stripe from lateral edge of postclypeus, through antennal base to compound eye; median mesonotal lobe with medium brown band along mid-line; lateral mesonotal lobes medium brown except along mid-line and along anterior border; medium brown lateral band on pro- and mesopleuron, reddish brown at sutures. Antennae medium brown. Compound eyes black. Abdomen as described in diagnosis. Forewing generally pale brown with colorless spot including stigmasac and another including r-m crossvein. Each longitudinal vein ending in darker spot bordering wing margin except R_1. Vein M-Cu and Cu_1 darker brown than surrounding membrane and darkly bordered, likewise vein R from Sc junction to radial fork and short distance along branches of fork, also R_1 darkened for short distance beyond stigmasac. Anal cells darker than surrounding membrane. Hindwing generally pale brown, palest throughout cells R_1 and R_3 and along posterior wing margin in cell M.

Female. — Measurements (Table I).

Morphology. — Subgenital plate typical of the genus. Ovipositor valvulae as described and figured for *T. luciensis.* Sclerite of spermathecal opening (fig. 55) as described in diagnosis. Paraproctal sensorium essentially same as in male.

Color (in alcohol). — Same as in male.

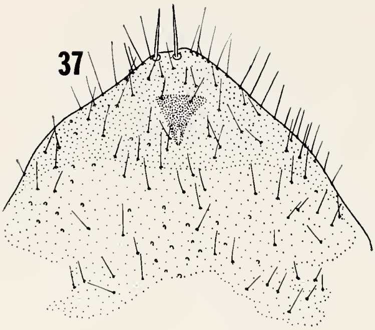
Type locality. — New Power Plant, 5 miles north of Roseau, Dominica, W.I., August 17, 1961, E. L. Mockford collector. Holotype ♂, allotype ♀, and 1 ♂ paratype. The types are in the author's collection.

Records. — Dominica: Portsmouth.

Habitat. — One of the specimens from the type locality was beaten from club moss. The habitat was not noted for the others.

Troctopsocopsis luciensis, new species

Diagnosis. — Abdomen free of reddish brown pigment except for small mark on each side at base. Male with uninterrupted comb of posterior clunial margin composed almost entirely of long teeth, only one or two lateral teeth being short. Sclerite of spermathecal opening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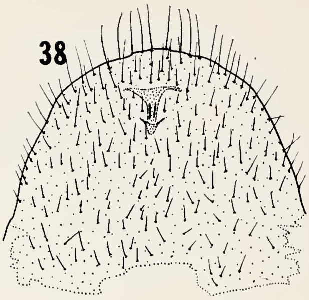
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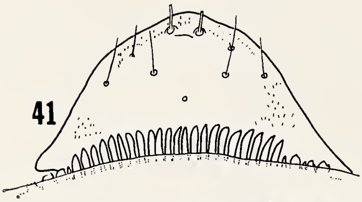
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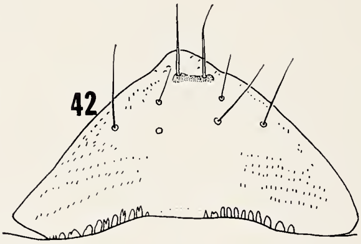
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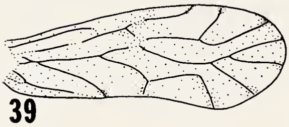
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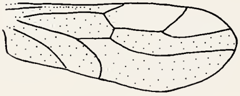
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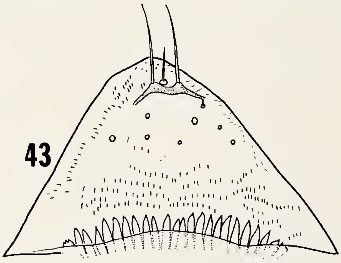
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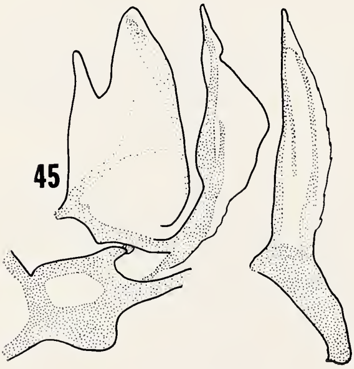
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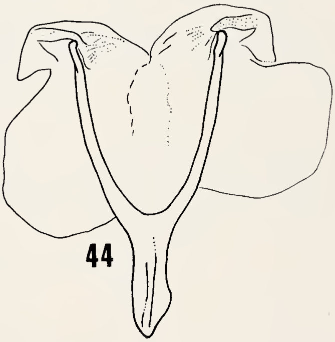
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Mockford — Electrentomoid psocids

with complete, wide peripheral ring.

Male. — Measurements (Table I).

Morphology. — Lacinial tip (fig. 57): lateral cusp with two denticles set at decided angles to cusp; bluntly pointed denticle at base of cusp. Hypandrium with distal margin approximately straight. Phallosome typical of the genus. Clunial comb (fig. 43) as described in diagnosis. Paraproctal sensorium with field of 6-8 trichobothria and 1-2 setae without basal rosettes.

Color (in alcohol). — Except for abdomen, almost exactly as in *T. martinicus*, the chief differences as follows: a distinct brown spot antero-mesad to each compound eye; pair of spots below ocelli distinctly separate; lateral thoracic stripe generally with less reddish brown, especially paler on prothorax. Wing markings same as in *T. intermedius*.

Female. — Measurements (Table I).

Morphology. — Subgenital plate typical of the genus. Ovipositor valvulae (fig. 45) with first valvula bearing anterior process from base of shaft, this process in contact with sclerite of spermathecal opening. Sclerite of spermathecal opening (fig. 56) as described in diagnosis. Paraproctal sensorium same as in male.

Color (in alcohol). — Same as in male.

Type locality. — Savanne Edmund, St. Lucia, W.I. (elevation approximately 600 m.), August 23, 1961, E. L. Mockford collector. Holotype ♂, allotype ♀, 8 ♂ and 9 ♀ paratypes and 8 nymphs. The types are for the present in the author's collection.

Habitat. — The type series was beaten from dead fern leaves on the edge of a road bordering a forested region.

Genus **Troctopsocus**, new name

Plaumannia Roesler, 1940, Zool. Anz. 129:236, *nec* Lundblad, 1936, Zool. Anz. 115:30.

Diagnosis. — Antennae of 13 segments. Pterostigma open basally. First segment of Rs in hindwing present. Frons longer than post-

EXPLANATION OF PLATE 21

Fig. 37. — *Protroctopsocus enigmaticus*, n. sp., ♀, subgenital plate.
Fig. 38. — *Troctopsoculus morenus*, n. sp., ♀, subgenital plate.
Fig. 39. — *Troctopsocopsis martinicus*, n. sp., ♀, forewing.
Fig. 40. — *T. martinicus*, n. sp., ♀, hindwing.
Fig. 41. — *T. martinicus*, n. sp., ♂, epiproct and clunial comb.
Fig. 42. — *T. intermedius*, n. sp., ♂, epiproct and clunial comb.
Fig. 43. — *T. luciensis*, n. sp., ♂, epiproct and clunial comb.
Fig. 44. — *T. luciensis*, n. sp., ♂, phallosome.
Fig. 45. — *T. luciensis*, n. sp., ♀, ovipositor valvulae.

clypeus in anterior view of head. Pretarsal claws as in *Troctopsocopsis.* Terminal segment of maxillary palpus elongate, rounded apically (fig. 49). M-cu crossvein present in forewing. Subgenital plate with posterior margin tapering, bearing 4 stout setae in middle; with T-shaped sclerite. Phallosome a simple Y-shaped structure.

Type species. — *Plaumannia separata* Roesler.

Troctopsocus separatus (Roesler)

Plaumannia separata Roesler, 1940, Zool. Anz. 129:236-237, figs. 15-20.

(Note: Specimens from Trinidad, W.I., described below, are assumed to be this species. They agree essentially with Roesler's figures of wing markings, and they agree as closely as is likely with Roesler's figures of lacinial tip and ovipositor valvulae. They average generally slightly smaller than Roesler's Brazilian specimens).

Diagnosis. — Wing markings essentially as illustrated by Roesler (1940: 236, fig. 15). Spermathecal sac with short, slender basal region and a constriction between this region and wide distal region. Ovipositor valvulae: basal arms of first and second valvulae much longer than in *T. similis,* n. sp.; secondary lobe of third valvula only slightly spinose.

Male: Measurements (Table I).

Morphology. — Hypandrium with posterior margin gently curved. Phallosome typical of the genus (as in fig. 63). Posterior margin of clunium bordering epiproct slightly thickened and with slightly scalloped edge, interrupted by smooth edge in middle. Epiproct with postero-mesal field of tiny papillae. Paraproctal sensorium with 7 trichobothria and 2 setae without basal rosettes.

Color (in alcohol). — Differing from Roesler's description only as follows: stripe from eye to mandibular base reddish brown; in addition to central spot from ocelli to clypeus, each lateral edge of frons with a (pale brown) spot; vertex with longitudinal brown stripe immediately to each side of midline, but pale on midline. Reddish brown spots on abdomen distributed as a latero-ventral series on each side (one spot per series per segment) including segments 1 to 4; ventral transverse bands connecting the spots in segments 1 and 2; small spot surrounding each spiracle in segments bearing spiracles.

Female: Measurements (Table I).

Morphology. — Lacinial tip (fig. 68) with lateral cusp bearing two appressed denticles. Subgenital plate with apex less tapering than in *T. similis* and *T. bicolor.* Ovipositor valvulae (fig. 59) as described in diagnosis. Paraproctal sensorium with 7 trichobothria and 2 setae without basal rosettes or with these poorly developed.

Color (in alcohol). — Same as in male.

Type locality. — Nova Teutonia, Santa Catharina, Brazil.

Records. — St. Pat's, Arima Valley, Trinidad, W.I.

Habitat. — Some of the specimens from the type locality were reported as taken on bark. The Trinidad specimens were beaten from dried fern leaves.

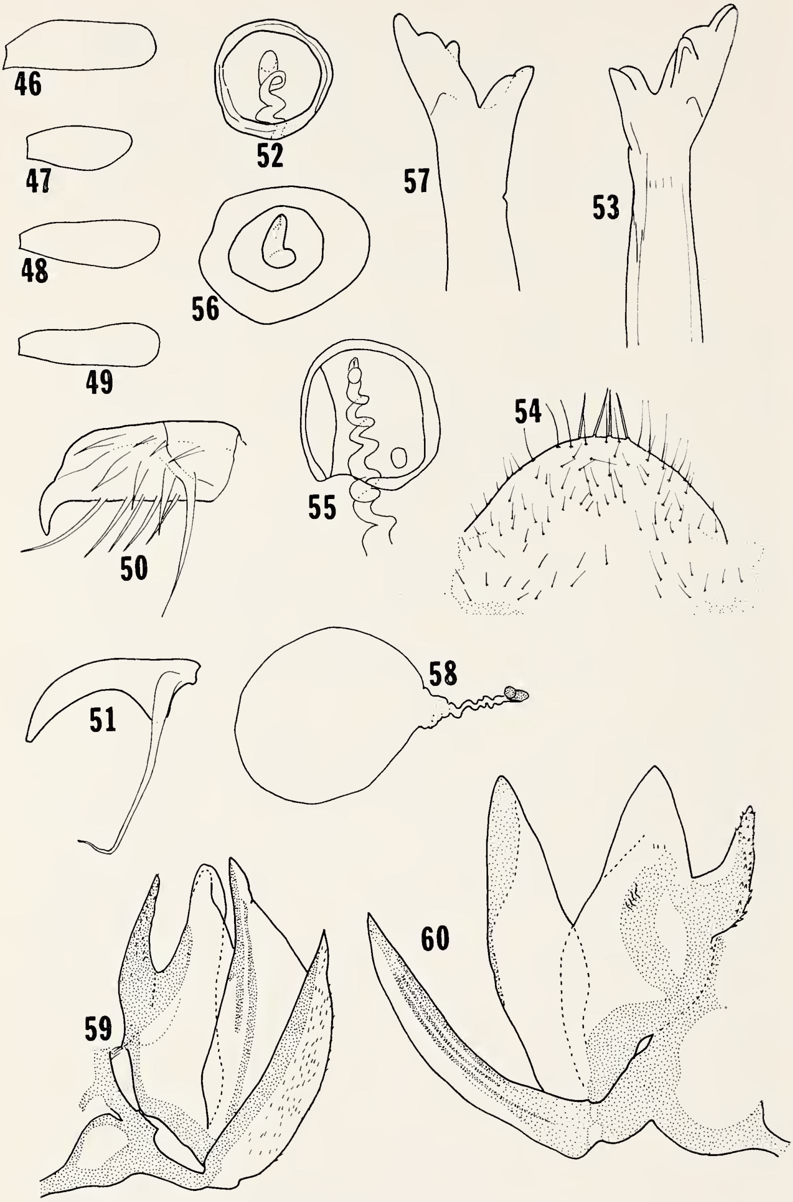
Troctopsocus similis, new species(♀)

Diagnosis. — Wing markings essentially same as in *T. separatus* (Roesler). Spermathecal sac with long slender basal region and no constriction between wide and slender regions. Ovipositor valvulae: basal arms of first and second valvulae very short; secondary lobe of third valvula exceedingly spinose.

Female. — Measurements (Table I).

Morphology. — Lacinial tip (fig. 70) with median cusp distinctly bidenticulate, lateral cusp with divided apex, 2 preapical denticles, one short and rounded, other longer, more slender, and protruding at an angle from cusp. Subgenital plate as described for the genus, and as figured for *T. bicolor*. Stem of T-shaped sclerite curved in preparation. Ovipositor valvulae (fig. 59) as described in diagnosis. Paraproctal sensorium with 7 trichobothria and 2 setae without basal rosettes.

Color (in alcohol). — Head, thorax, and legs largely dull ivory yellow. Head extensively marked with medium brown as follows: a broad band on each side of epicranial suture, each band bending laterally just before reaching lateral ocellus to end at antero-mesal margin of compound eye. Compound eyes bordered by medium brown spots. Frons bordered ventrally and laterally with medium brown and in middle with medium brown mark in form of rounded letter M. Genae behind antennal bases marked with reddish brown. Compound eyes black. Antennae reddish brown. Thorax marked on each side with 3 longitudinal parallel stripes of reddish brown, the lowest one mostly confined to coxal bases. Thorax dorsally extensively marked with reddish brown, but sutures and an elongate central spot dull ivory yellow. Abdomen with entire ventral surface dark reddish brown except for colorless posterior half of subgenital plate. Sides of abdomen dull ivory yellow, somewhat darker on clunium. Abdomen dorsally pale reddish brown. Posterior margins of epiproct and paraprocts reddish brown. Cell R_1 of forewing in region underlying distal end of pterostigma and wing margin mostly



Mockford — Electrentomoid psocids

colorless. Otherwise, wings marked as in *T. separatus* (Roesler).

Type locality. — 6 miles west of Macuspana, Tabasco, Mexico, April 3, 1964, E. L. Mockford collector. Holotype ♀, 1 ♀ paratype, and 8 nymphs. The types are in the author's collection.

Habitat. — The specimens were beaten from foliage of broad-leaved trees, shrubs, and palms in lowland rain forest.

Troctopsocus bicolor, new species

Diagnosis. — Forewing marked (fig. 61) with a colorless band running through median cells and areola postica.

Male. — Measurements (Table I).

Morphology. — Hypandrium with posterior margin slightly curved. Phallosome fig. 63) typical of the genus. Clunium and epiproct unadorned. Paraproctal sensorium with 7-8 trichobothria with well developed basal rosettes and 3-4 with weakly developed rosettes.

Color (in alcohol). — Body and legs pale reddish brown. Antennae somewhat darker reddish brown. Compound eyes dark reddish brown. Wings (figs. 61, 62) with veins white, membrane reddish brown except colorless band running diagonally across median cells and areola postica. Hindwing faint reddish brown except median cell colorless in its distal two-thirds.

Female. — Measurements (Table I).

Morphology. — Lacinial tip (fig. 65) with lateral cusp bidenticulate; median cusp with tip apparently not divided, 2 denticles below

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Explanation of Plate 22

Fig. 46. — *Protroctopsocus enigmaticus,* n. sp., ♀, distal segment of maxillary palpus.
Fig. 47. — *Troctopsoculus morenus,* n. sp., ♀, distal segment of maxillary palpus.
Fig. 48. — *Troctopsocopsis martinicus,* n. sp., ♀, distal segment of maxillary palpus.
Fig. 49. — *Troctopsocus separatus* (Roesler), ♀, distal segment of maxillary palpus.
Fig. 50. — *Troctopsocopsis martinicus,* n. sp., ♀, anterior claw of posterior pretarsus.
Fig. 51. — *T. martinicus,* n. sp., ♀, posterior claw of posterior pretarsus.
Fig. 52. — *T. martinicus,* n. sp., ♀, sclerite of spermathecal opening.
Fig. 53. — *T. martinicus,* n. sp., ♀, lacinial tip.
Fig. 54. — *T. martinicus,* n. sp., ♀, subgenital plate.
Fig. 55. — *T. intermedius,* n. sp., ♀, sclerite of spermathecal opening.
Fig. 56. — *T. luciensis,* n. sp., ♀, sclerite of spermathecal opening.
Fig. 57. — *T. luciensis,* n. sp., ♂, lacinial tip.
Fig. 58. — *T. luciensis,* n. sp., ♀, spermatheca.
Fig. 59. — *Troctopsocus separatus* (Roesler), ♀, ovipositor valvulae.
Fig. 60. — *T. similis,* n. sp., ♀, ovipositor valvulae.

tip at very different levels, the lower one standing out from the cusp. Subgenital plate with apex only slightly tapering (fig. 64); arms of T-shaped sclerite obscure laterally. Ovipositor valvulae (fig. 66): first and second valvulae with long, slender stems; secondary lobe of third valvula beset with numerous tiny slender spines. Paraproctal sensorium with 8 trichobothria and 2 setae without basal rosettes.

Color (in alcohol). — Same as in male.

Type locality. — Chorroni Pass, Coast Range, Aragua, Venezuela (elevation 1550 m.), March 7, 1959, E. L. Mockford and C. J. Rosales collectors. Holotype ♂, allotype ♀, 3 ♀ paratypes, and 3 nymphs. The holotype, allotype, and 1 ♀ paratype will be deposited in the American Museum of Natural History, New York City. Remaining paratypes will be retained in the author's collection.

Habitat. — The type series was beaten from dried fern leaves in upland rain forest openings.

Family **Manicapsocidae,** new family

Diagnosis. — Antennae of 15 segments. Frontal sutures absent. Lacinial tip with lateral cusp curved outward and bearing a few indistinct, rounded denticles. No row of denticles on anterior carina of first femur. Tarsi three-segmented. Pretarsal claws each with a single preapical denticle. Pterostigma closed basally. Vein 2A of forewing joining wing margin distally or joining vein 1A. First segment of Rs in hindwing absent. Third ovipositor valvula not or only very slightly bilobed apically. Shades of red prominent in body coloration.

Genus *Manicapsocus* Smithers

Manicapsocus Smithers, 1965, Journ. Ent. Soc. S. Afr., 28:46

Diagnosis. — Vein 2A joining wing margin. Frons (from median ocellus to border with postclypeus) about equal in length to postclypeus. First flagellar segment curved. R_1 greatly expanded near wing margin, forming a dark spot. Epicranial plates raised into knobs mesad of compound eyes.

Type species. — *M. alettae* Smithers (Angola).

Genus **Epitroctes,** new genus

Diagnosis. — Vein 2A joining 1A. Adults dimorphic, males macropterous and females micropterous. Frons longer than postclypeus in anterior view of head. Male forewings only very slightly marked (fig. 72). First flagellar segment curved, tapering slightly from base to tip. Mesothoracic tergal lobes of male protruding only slightly above a line drawn from vertex to dorsal surface of abdomen.

Type species. — *E. tuxtlarum,* new species.

Epitroctes tuxtlarum, new species

Male. — Measurements (Table I).

Morphology. — Lacinial tip (fig. 74) with median cusp single; lateral cusp with tip undivided; two distinct rounded denticles arising at different levels below tip and a third very indistinct denticle arising nearer tip; base of lateral cusp with a curved ridge. Hypandrium with distal margin slightly curved, region of margin beset with numerous setae. Phallosome (fig. 75) with parameres joined anteriorly to form a long rod with a more slender posterior extension beyond the point of junction of the parameres. Each paramere branching, the more lateral pair of branches curving around and abutting on each other posteriorly and each bearing a thumb-shaped process lateral to abutment; the more median branches each running straight a distance then curving to form spoon-shaped end to side of basally more lateral branch. Paraproctal sensorium with 10-11 setae, none with basal rosettes.

Color (in alcohol). — Head generally pale grayish brown, with pair of longitudinal white stripes through vertex and white spot including ocelli; two small red spots bordering compound eye ventrally and a broken red band across gena. Ocelli rimmed in red: the laterals mesally, the median dorsally. Compound eyes purple, beset with deep reddish-purple spots roughly arranged in bands across eye, each spot at base of a tiny seta. Sclerotized portions of thorax generally pale grayish brown. Well colored individual with a red lateral band running length of thorax each side. Red band across base of each coxa. Legs generally grayish brown; each femur with a red spot near distal end; each tibia with 2 reddish brown bands, one at about one-fourth distance from base, other at about three-fourths distance from base. Abdomen basad of clunium generally pale grayish brown dorsally and ventrally with a broad red band (continuous to tip) on each side; base with a rounded, well sclerotized dark brown spot dorsally; clunium, hypandrium, epiproct and paraprocts medium brown in cuticle, the red band running through each side subcuticularly to tip of each paraproct. Wings fumose, more deeply so in base of pterostigma and base of areola postica.

Female. — Measurements (Table I).

Morphology. — Subgenital plate (fig. 76) with posterior margin rounded; T-shaped sclerite with arms broad and diffuse. Ovipositor valvulae (fig. 77): third valvula with notch near apex marking presence of secondary lobe. Spermatheca (fig. 78): sac of two distinct regions separated by a constriction, the part proximal to the duct a narrow, tapering, curved neck. Paraproctal sensorium with 8 setae, none with true basal rosettes.

Color (in alcohol). — Head same as in male except frons grayish white with two pale grayish brown spots below ocelli. Thorax same as in male except for presence of a red band running length of thorax on dorsal midline. Abdomen same as in male except that dark brown dorsal spot at base much larger, covering all of first two terga.

Type locality. — Upland rain forest 8 miles northwest of Santiago Tuxtla, Veracruz, Mexico (Sierra de las Tuxtlas), June 24, 1966, E. L. Mockford collector. Holotype ♂, allotype ♀, 2 ♂ paratypes, and 1 nymph. Types are in the author's collection.

Habitat. — These insects were found on the trunk of a large tree with buttressed base deep in the upland rain forest. On the same trunk in the immediate vicinity of these specimens were several species of Ptiloneurid psocids.

Discussion. — A single female, probably representing a distinct species of this genus, was taken at Chorroni, Aragua State, Venezuela, in the coastal mountains. Like the Mexican female, it is micropterous.

Family **Compsocidae**, new family

Diagnosis. — Antennae of 13 or 14 segments. Frontal sutures present. Lacinial tip with lateral cusp curved outward and bearing a few indistinct, rounded denticles. Row of denticles present on anterior carina of first femur. Tarsi three-segmented. Pretarsal claws each with two preapical denticles. Mesothoracic tergal lobes not protruding above a line drawn from vertex of head to dorsal

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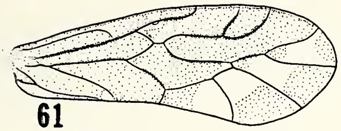
EXPLANATION OF PLATE 23

Fig. 61. — *Troctopsocus bicolor,* n. sp., ♀, forewing.
Fig. 62. — *T. bicolor,* n. sp., ♀, hindwing.
Fig. 63. — *T. bicolor,* n. sp., ♂, phallosome.
Fig. 64. — *T. bicolor,* n. sp., ♀, subgenital plate.
Fig. 65. — *T. bicolor,* n. sp., ♀, lacinial tip.
Fig. 66. — *T. bicolor,* n. sp., ♀, ovipositor valvulae.
Fig. 67. — *T. separatus* (Roesler), ♀, spermatheca.
Fig. 68. — *T. separatus* (Roesler), ♀, lacinial tip.
Fig. 69. — *T. similis,* n. sp., ♀, spermatheca.
Fig. 70. — *T. similis,* n. sp., ♀, lacinial tip.
Fig. 71. — *Epitroctes tuxtlarum,* n. sp., ♂, pretarsal claw.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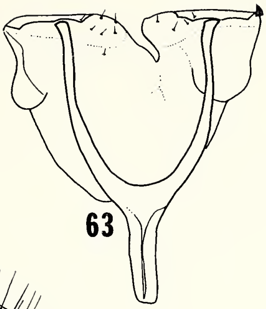
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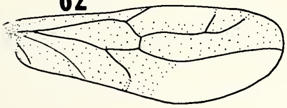
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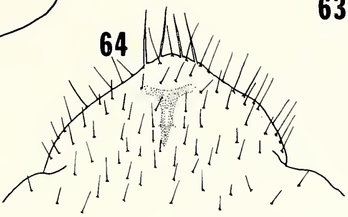
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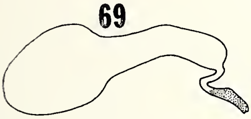
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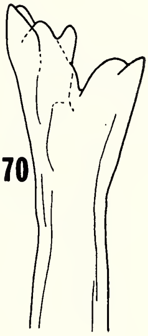
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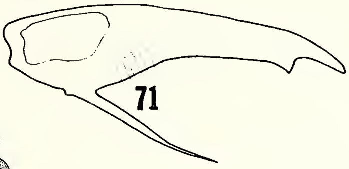
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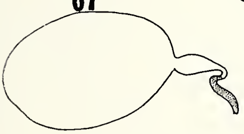
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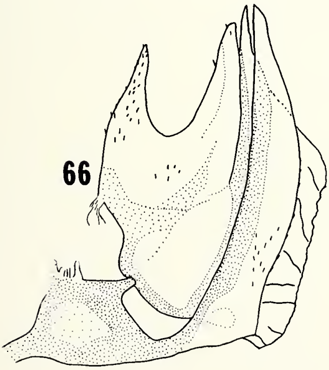
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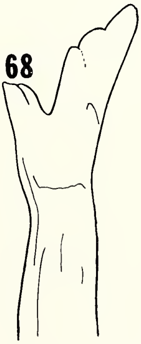
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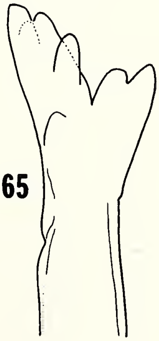
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MOCKFORD — ELECTRENTOMOID PSOCIDS

surface of abdomen. Pterostigma closed basally. Vein 2A of forewing joining vein 1A. First segment of Rs in hindwing present or absent. Vein M in hindwing one-branched. Third ovipositor valvula deeply bilobed apically.

Genus *Compsocus* Banks

Compsocus Banks, 1930, Psyche, 37:183.

Diagnosis. — Antennae of 14 segments. Frons approximately equal in length with postclypeus in anterior view. Pretarsal claws each with two preapical teeth. First segment of Rs in hindwing present. Minute scale-like structures present on forewing surfaces. Spermathecal duct straight.

Type species. — *C. elegans* Banks.

Compsocus elegans Banks

Compsocus elegans Banks, 1930, Psyche 37:183-184, pl. 9, fig. 4.

Male. — Measurements (Table I).

Morphology. — Lacinial tip (fig. 89) with median cusp slightly divided; lateral cusp with apex simple, bearing two low, rounded denticles rising at same level near apex. Anterior femur with row of 15-16 denticles (fig. 79), some of them bifid. Hypandrium (fig. 84) with apical margin curved, slightly impressed in middle. Phallosome (fig. 85) in form of letter Y but closed posteriorly, the stem about half length of arms; each arm dividing about halfway along its length to produce a more membranous lateral branch and a more sclerotized median branch, the lateral branch terminating as a sac surrounding median branch and becoming closely associated medially with complex apical sclerites of phallosome; this sac bearing field of pores on outer margin near its posterior end. Paraproctal sensorium with 5-6 trichobothria and 7 shorter setae lacking basal rosettes. Epiproct with field of closely set rather stout setae at its tip.

Color (in alcohol). — not recorded except for wing pattern, due to very poor condition of specimen. Forewing (fig. 82) complexly mottled with gray, pale brown, and colorless spots, the gray mostly in 5 transverse spots: an obscure one at wing tip, a small one from distal end of cell R_1 through cell R_3 and cell R_5; a large one covering most of pterostigma and extending posteriorly through base of cell M_2; slender one from wing margin just basad of pterostigma back through cell M_3; wide one from middle of costal cell through anal cells just basad of nodulus; remainder of wing membrane largely pale brown except for 3 colorless (or nearly so) spots: one through tip of areola postica extending up across cell M_3 another along vein Cu_1a, another through nodulus. Hindwing washed with pale brown, unmarked.

Female. — Measurements (Table I).

Morphology. — Anterior femur with many more denticles in row than in male (39 in single femur observed). Subgenital plate (fig. 86) with posterior margin tapering toward apex, the apex bearing two long, stout setae; T-shaped sclerite with pair of lateral extensions arising along stem near its base. Ovipositor valvulae (fig. 87). Spermatheca (fig. 88) with no constriction separating the two regions of its sac; basal region very small; wall of sac beset with small rings of minute, inward-directed spines; sclerite of spermathecal orifice a V-shaped structure with a sclerotized band bisecting the angle of the V; actual orifice near apex of the V. Paraproctal sensorium with 12-13 setae, none with well developed basal rosettes.

Color (in alcohol). — Head, legs, and mesothoracic dorsum dark brown. Compound eyes gray showing faintly three transverse brown bands. Metathorax dorsally and entire thorax laterally medium brown. Preclunial portion of abdomen ventro-laterally medium brown with reddish hue, pale brown dorsally and ventrally. Subgenital plate and clunium medium brown mottled with darker brown. Wings marked as in male, the pale brown areas of forewing with silvery sheen in reflected light.

Type locality. — Barro Colorado Island, Panama Canal Zone.

Records. — Mexico. *Chiapas:* Palenque Ruins. Panama Canal Zone. Fort Sherman.

Habitat. — Mexican specimens, two females and seven nymphs, were taken on trunks of large forest trees with buttressed bases. They sit on the surface of bark and run rapidly when disturbed.

Genus **Electrentomopsis,** new genus

Diagnosis. — Antennae of 13 segments. Frons only very slightly longer than postclypeus in anterior view. Micro-vestiture of forewing minute points. Spermathecal duct coiled spring-like.

Type species. — *E. variegatus*, new species.

Electrentomopsis variegatus, new species

Male. — Measurements (Table I).

Morphology. — Pit containing antennal base particularly deep and conical as seen in cleared head. Sculpture of integument of frons and vertex a net of polygonal areas (mostly hexagonal) set off by lines. Compound eyes with transverse rows of scattered tiny setae. Lacinial tip (fig. 90) with simple median cusp; lateral cusp with apex simple, broadly rounded; one large, rounded denticle below apex, and apparently one smaller one at same level on opposite edge; a ridge at base of lateral cusp. Anterior femur with row of 13 spines, irregularly spaced, along anterior carina (fig. 91). Hypandrium with posterior margin rounded and bearing numerous setae, two close to center longer than others. Phallosome (fig. 100): parameres in form of letter Y, the stem formed of fused bases; around posterior end of each arm a membranous sac, slightly sclerotized posteriorly and beset posteriorly and medially with rounded pores; these sacs apparently continuous medially with endophallus, a bilobed sac containing on its inner wall several longitudinal rows of denticles fused to form saw-blade-like structures. Paraproctal sensorium with 5-6 setae with poorly developed basal rosettes and 4-5 without basal rosettes.

Color (in alcohol). — Head with flattened dorsal part of vertex gray, anterior face of vertex dark reddish brown in upper half, separated from gray dorsum by white transverse stripe, the reddish brown region containing two white spots, one near each compound eye; lower half of anterior face of vertex grayish orange; upper half of frons white mottled with gray, the included median ocellus dark brown, this white region partially separated from bright orange lower half of frons by a line of reddish brown spots. Postclypeus pale grayish green mottled near its upper border with dark reddish brown; gena white with reddish brown stripe below compound eye and another just above base of mandible. Antennae dark brown. Compound eyes bright yellowish green with 6 transverse bands of darker green, each darker band including one of the rows of tiny setae, each seta arising from a tiny dark brown spot. Mesothorax dorsally yellowish green mottled with few reddish brown spots. Metathorax dorsally reddish brown. Thorax laterally white mottled with reddish brown. Anterior and middle coxae and femora pale gray, the femora

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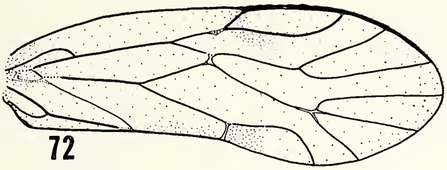
EXPLANATION OF PLATE 24

Fig. 72. — *Epitroctes tuxtlarum,* n. sp., ♂, forewing.
Fig. 73. — *E. tuxtlarum,* n. sp., ♂, hindwing.
Fig. 74. — *E. tuxtlarum,* n. sp., ♂, lacinial tip.
Fig. 75. — *E. tuxtlarum,* n. sp., ♂, phallosome.
Fig. 76. — *E. tuxtlarum,* n. sp., ♀, subgenital plate.
Fig. 77. — *E. tuxtlarum,* n. sp., ♀, ovipositor valvulae.
Fig. 78. — *E. tuxtlarum,* n. sp., ♀, spermatheca.
Fig. 79. — *Compsocus elegans* Banks, ♂, anterior femur.
Fig. 80. — *C. elegans* Banks, ♀, pretarsal claw.
Fig. 81. — *Electrentomopsis variegatus,* n. sp., ♂, pretarsal claw.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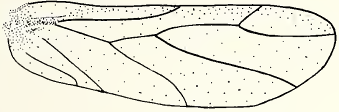
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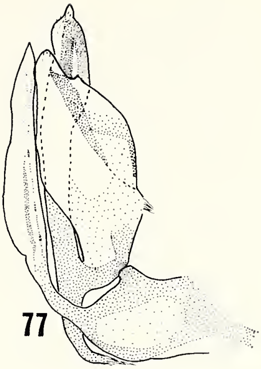
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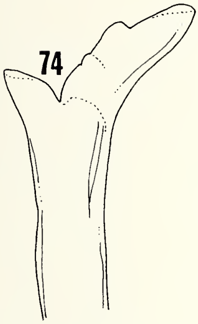
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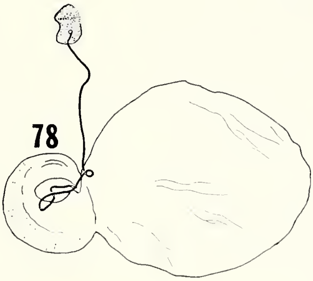
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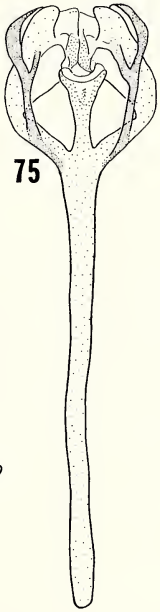
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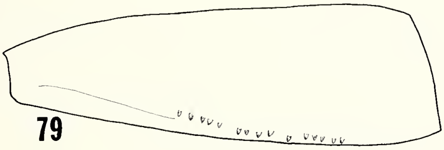
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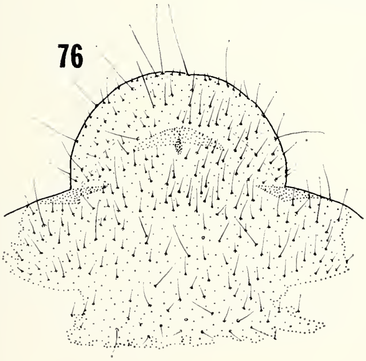
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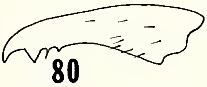
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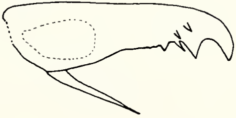
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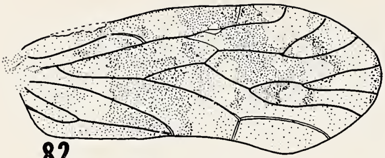
Mockford — Electrentomoid psocids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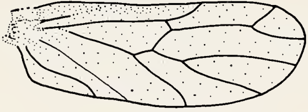
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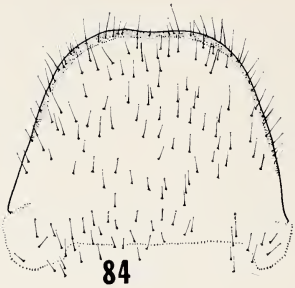
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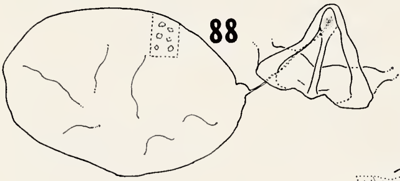
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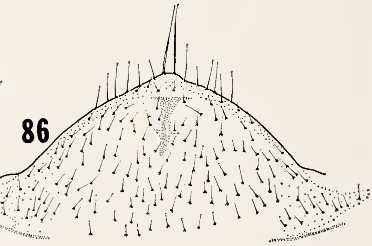
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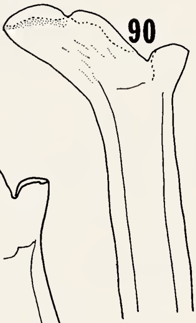
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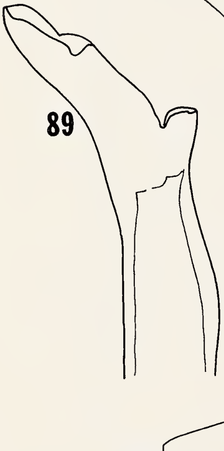
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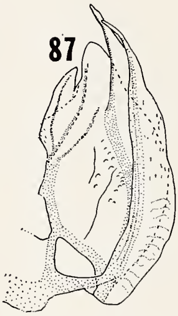
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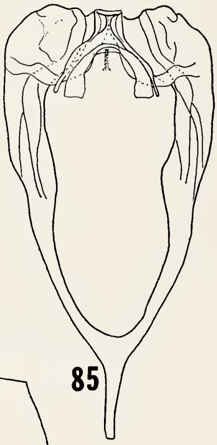
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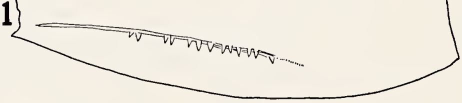
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each with two dark brown bands, one through middle and one through distal end. Anterior and middle tibiae and tarsi largely pale brown, tibiae each with basal and subapical dark brown bands and apical white band; tarsi each with basal dark band and with second segment darker than region basal or distal to it. Posterior coxae medium brown; posterior femora each mostly dark brown with pale gray apical band; posterior tibia largely pale gray with irregular brown spots along outer face and a dark brown band just distal of middle. Abdomen white along sides, mottled dark brown and pale brown dorsally with a largely dark brown band including most of terga 2 through 4; ventrally mottled with dark brown, white, and a colorless region underlying seminal vesticles; a mottled, largely dark brown band including sterna 2 through 4; hypandrium dark brown; clunium pale brown mottled with reddish brown; epiproct and paraprocts white mottled with dark brown. Forewing (fig. 98) with brown and grayish brown spots: one at end of each logitudinal vein, two in costal cell, a series forming an arc with one each in cells R_1, R_3, R_5, M_1 and M_2, a large pale one partly in base of cell R_5 but largely in cell M_3, a dark one through areola postica extending forward into cell M_3, and a few other minor ones. Hindwing (fig. 99) unmarked, clear.

Female. — Measurements (Table I).

Morphology. — Subgenital plate (fig. 101) tapering toward apex, the apex somewhat truncated and bearing 2-3 setae longer and stouter than others; T-shaped sclerite vague, lacking arms. Ovipositor valvulae (fig. 102) with first and second valvulae closely associated along their median edges with sclerite or orifice of spermatheca; third valvula deeply bilobed. Spermatheca (fig. 103) with sac composed of two regions, both elongated, the one further from duct expanded in its blind end. Paraproctal sensorium with 2 setae

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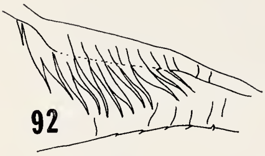
EXPLANATION OF PLATE 25

Fig. 82. — *Compsocus elegans* Banks, ♂, forewing.
Fig. 83. — *C. elegans* Banks, ♂, hindwing.
Fig. 84. — *C. elegans* Banks, ♂, hypandrium.
Fig. 85. — *C. elegans* Banks, ♂, phallosome.
Fig. 86. — *C. elegans* Banks, ♀, subgenital plate.
Fig. 87. — *C. elegans* Banks, ♀, ovipositor valvulae.
Fig. 88. — *C. elegans* Banks, ♀, spermatheca (dotted lines enclosing example of surface sculpture which is same over entire spermatheca).
Fig. 89. — *C. elegans* Banks, ♂, lacinial tip.
Fig. 90. — *Electrentomopsis variegatus*, n. sp., ♂, lacinial tip.
Fig. 91. — *E. variegatus*, n. sp., ♂, anterior femur.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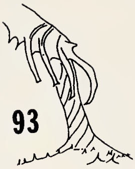
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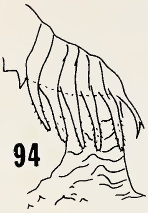
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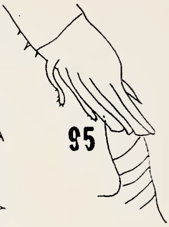
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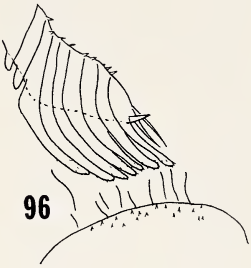
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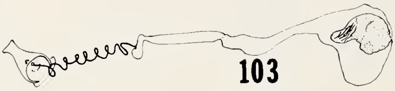
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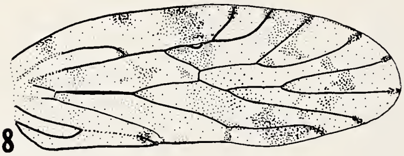
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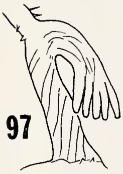
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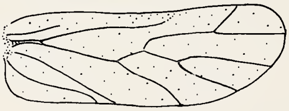
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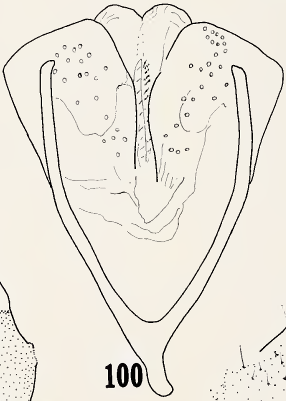
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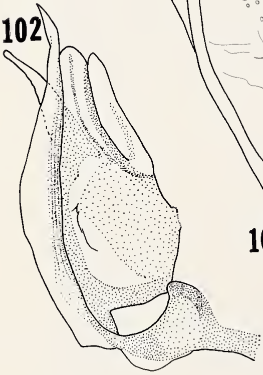
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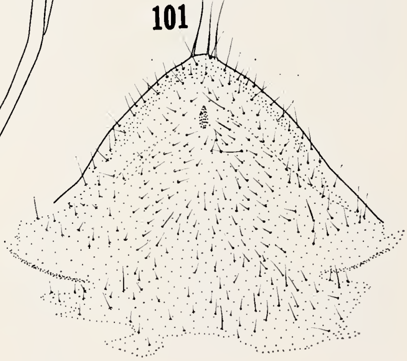
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with basal rosettes, 4 setae each with a narrow unsculptured ring around its socket, and 4 setae with neither basal rosette nor unsculptured ring.

Color (in alcohol). — Essentially same as in male.

Type locality. — Ejido Libertad, about 4 miles west of Frontera, Tabasco, Mexico, June 27 and July 3, 1966, E. L. Mockford, R. Sloan, and A. Manzano collectors. Holotype ♂, allotype ♀, 6 ♂ and 2 ♀ paratypes and 5 nymphs. Types are at present in author's collection.

Habitat. — This species was taken on trunks of large trees with buttressed bases in lowland rain forest. These insects sit on the surface of bark and run rapidly when disturbed.

Genera Incertae Sedis

Genus *Electrentomum* Enderlein

Electrentomum Enderlein, 1911. Palaeontographica 58:337.

Diagnosis. — Antennae of 13 segments. Frontal sutures absent. Lacinial tip with lateral cusp curved outward and bearing a few indistinct, rounded denticles. Tarsi three-segmented. Pretarsal claws each with a single preapical denticle. Pterostigma closed basally. Vein 2A of forewing joining vein 1A. First segment of Rs in hindwing absent.

Type species: *E. klebsianum* Enderlein (Baltic amber).

Note: Enderlein's statement (1911:338) "1. *Hintertarsenglied mit ca.* 21 *Ctenidiobothrien*" is apparently in error. His figure of the posterior tarsus (Pl. XXIV, Fig. 75) shows only ordinary bristles without basal ctenidia. Compare his figure 52 on the same plate showing a psocid with ctendiobothria.

EXPLANATION OF PLATE 26

Fig. 92. — *Thylacopsis* sp. (Suborder Trogiomorpha), in-flight wing clasp.
Fig. 93. — *Musapsocus creole*, n. sp., ♀, in-flight wing clasp.
Fig. 94. — *Protroctopsocus enigmaticus*, n. sp., ♀, in-flight wing clasp.
Fig. 95. — *Electrentomopsis variegatus*, n. sp., ♂, in-flight wing clasp.
Fig. 96. — *Pseudoseopsis hellmani* Mock. and Gurn., ♀, in-flight wing clasp.
Fig. 97. — *Hemipsocus* sp. (Suborder Psocomorpha), in-flight wing clasp.
Fig. 98. — *Electrentomopsis variegatus*, n. sp., ♂, forewing.
Fig. 99. — *E. variegatus*, n. sp., ♂, hindwing.
Fig. 100. — *E. variegatus*, n. sp., ♂, phallosome.
Fig. 101. — *E. variegatus*, n. sp., ♀, subgenital plate.
Fig. 102. — *E. variegatus*, n. sp., ♀, ovipositor valvulae.
Fig. 103. — *E. variegatus*, n. sp., ♀, spermatheca.

Genus *Parelectrentomum* Roesler

Parelectrentomum Roesler, 1940. Zool. Anz. 129:228.

Diagnosis. — Differing from *Electrentomum* according to original description, by presence of first segment of Rs in hindwing, and relatively larger medial stem compared to medial branches in forewing.

Type species. — *P. prescum* Roesler (Baltic amber).

PHYLOGENETIC RELATIONSHIPS OF THE ELECTRENTOMOID PSOCIDS

Hennig (1966) has stressed the predictive value of phylogenetic classification and has emphasized that only apomorphous (derived) characters may be used for setting out monophyletic groups, while plesiomorphous (primitive) characters are useless for this purpose.

Phylogenetic problems of two sorts (taxonomic levels) are considered in this section. First, what are the phylogenetic relationships of the Electrentomoid families to other families of Psocoptera? Secondly, what are the phylogenetic relationships among the genera within the Family Troctopsocidae?

Enderlein (1911) placed *Electrentomum* as the sole representative of one branch of a basal dichotomy of the family Amphientomidae. Roesler (1944) recognized a distinct family Plaumanniidae for his genus *Plaumannia* (=*Troctopsocus*) and within the Amphientomidae recognized a subfamily Electrentominae for *Electrentomum* and *Parelectrentomum* and a subfamily *Compsocinae* for *Compsocus.* The remainder of the Amphientomidae were placed in two subfamilies, Amphientominae and Tineomorphinae.

Pearman (1936) set up a group Amphientometae which would encompass the taxa mentioned above.

We must decide first whether or not the Amphientometae is a phylogenetocally valid taxon, i.e. can it be characterized by at least a few apomorphous traits?

The group Amphientometae may be diagnosed as follows (modified from Badonel, 1951): Adults with three tarsal segments, antennae with 15 segments, the flagellar segments annulated; labial palpi one- or two-segmented; three, two, or no ocelli, well separated when present; forewings with pterostigma not thickened, with nodulus and second anal vein, and with apex rounded; coxal organ reduced to the mirror.

To this list may be added the following characters shared by a number of species of Amphientomidae with a number of species of electrentomoids, but not universal: Antennal socket sunk in a pit, the pit separated from frontoparietal region by a ridge; two median veins present in hindwing; Sc rejoining R in forewing; a ridge running length of anterior coxa along its antero-lateral surface; compound eyes transversely color banded; a row of spines or denticles on anterior carina of first femur; R forked in forewing immediately basal to pterostigma; a T-shaped sclerite or homologous structure present on subgenital plate; third valvula deeply bilobed; pretarsal claw with a longitudinal series of spines, setae, or minute ridges on its lower surface.

It is very difficult to decide which of the above conditions are plesiomorphous and which are apomorphous for the Amphientometae. Only two methods are available for solution of this problem: comparisons with fossil forms, and comparisons with other modern, presumably monophyletic groups of psocids and orders of other insects.

Comparison with the Permian psocids (Carpenter, 1933) shows that the following characters are probably plesiomorphous for the order: three tarsal segments; forewing with pterostigma not thickened, with second anal vein, and with apex rounded; antennal socket sunk in a pit, the pit separated from fronto-parietal region by a ridge (see Carpenter, 1933, fig. 13); Sc rejoining R in forewing.

Three other groups of psocids are available for comparison: Suborder Trogiomorpha, Group Nanopsocetae, and Suborder Psocomorpha. If they are monophyletic groups not including or included within the Amphientometae, they may be compared with the Amphientometae for testing plesiomorphy or apomorphy of characters.

The Suborder Trogiomorpha is probably monophyletic on the basis of the apomorphous character of considerable reduction of the first and second ovipositor valvulae and enlargement of the third valvula. The Group Nanopsocetae is probably monophyletic on the basis of small size and associated simplification of wing venation. The Suborder Psocomorpha is probably monophyletic on the basis of the thickened pterostigma and enlargement of the mesothorax.

In the classification generally in vogue at present, the Group Nanopsocetae is regarded as a sister group with the Amphientometae, the two groups composing the Suborder Troctomorpha. Although the Nanopsocetae is probably monophyletic, it is necessary to try to determine if it is phylogenetically coordinate with the Amphientometae or if a subordinance relationship may exist between the two.

This question can be answered in part on the basis of distribution of the nodulus. This structure, the distal junction of veins Cu_2 and 1A in the forewing, which bears the in-flight wing coupling device, is present in Group Psocatropetae (Suborder Trogiomorpha),

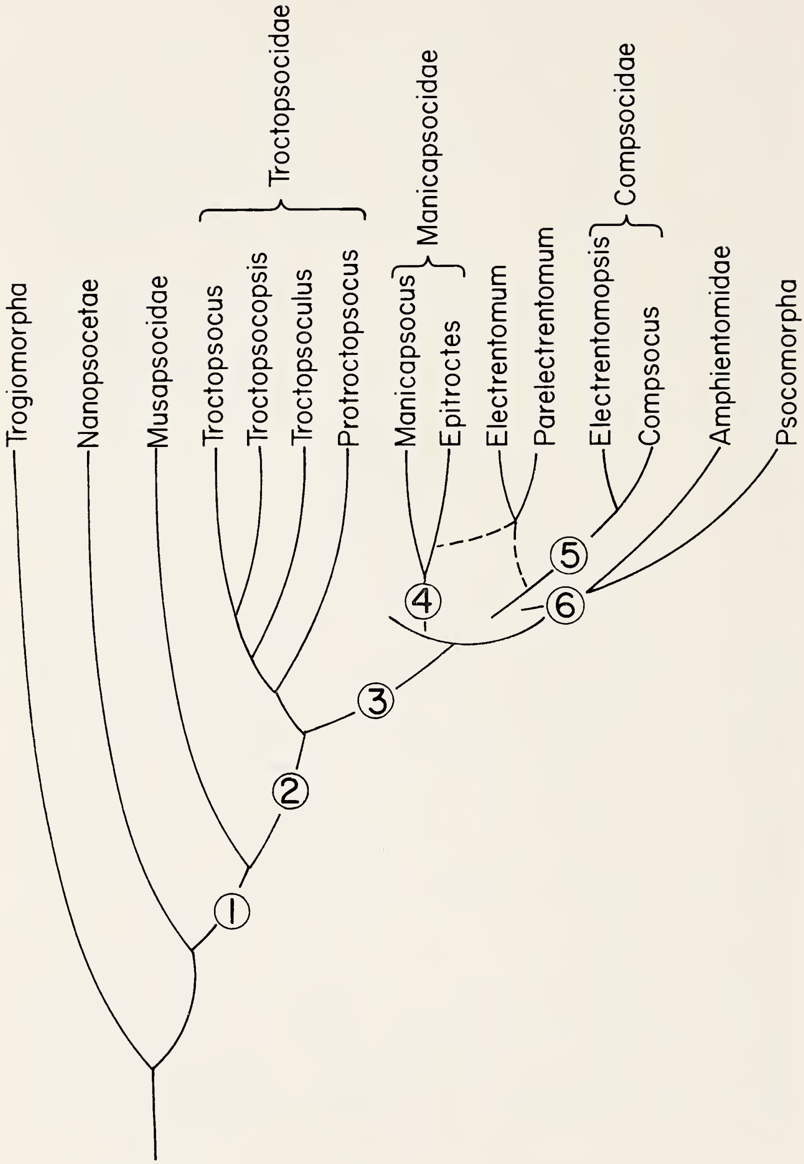
Trogiomorpha
Nanopsocetae
Musapsocidae
Troctopsocidae
Troctopsocus
Troctopsocopsis
Troctopsoculus
Protroctopsocus
Manicapsocidae
Manicapsocus
Epitroctes
Electrentomum
Parelectrentomum
Compsocidae
Electrentomopsis
Compsocus
Amphientomidae
Psocomorpha
1
2
3
4
5
6

FIGURE 104

Group Amphientometae, and Suborder Psocomorpha. It is apparently universally absent in the Permian fossil psocids, which strongly suggests that its absence is the plesiomorphous condition for the order, and that it has arisen several times independently (at least twice) within the order. Its absence in the Nanopsocetae rules out the possibility that this group is phylogenetically subordinate to the Amphientometae. At the same time its absence in most members of the Suborder Trogiomorpha establishes the same thing for that group, with regard to their relationship to the Amphientometae and to the Suborder Psocomorpha. The Trogiomorpha also cannot be subordinate to the Nanopsocetae, as they bear several plesiomorphous characters which the Nanopsocetae lack (M_3 present in forewing, Cu branched in hindwing.

The Suborder Trogiomorpha and the Group Nanopsocetae, then, appear to be valid monophyletic lines not included in the Amphientometae. At the same time, possession of a nodulus shows the Amphientometae to be a monophyletic group and its possession of vein 2A of the forewing shows it to be not included within either Trogiomorpha or Nanopsocetae.

It is now necessary to try to decide whether Suborder Psocomorpha is phylogenetically coordinate with the Amphientometae or if a subordinance relationship exists between them. On the basis of characters used above to establish monophyly of the Psocomorpha, the phylogenetic subordinance of the Amphientometae to the Psocomorpha is ruled out.

It must be noted that the Family Amphientomidae shares a number of characters with the Psocomorpha. These include tarsal ctenidiobothria, lacinia with lateral cusp curved out and bearing short denticles, and the greatly enlarged postclypeus, which is longer than frons in anterior view of face. These characters have good probability of being shared through synapomorphy, hence marking a monophyletic line.

Fig. 104. — Dendrogram showing probable phylogenetic relationships of major lines of Psocoptera and families and genera of Electrentomoid psocids. Numbers refer to following notations: (1) nodulus acquired; (2) third valvula bilobed apically; (3) lateral cusp of lacinial tip curved outward, bearing low, rounded denticles; (4) third valvular lobes reunited, spines or denticles of first femur absent; (5) vein M of hindwing branched, compound eyes color-banded; (6) tarsal ctenidiobothria present.

The assumption of such a line allows reasonable explanation of the evolution of the in-flight wing coupling mechanism, from a set of pointed, separated spines in the Trogiomorpha through truncated spines set close together in the Amphientomidae, to a hook composed of truncated spines fused at their bases in the Psocomorpha. If the electrentomoid families are placed along the line leading to the Amphientomid-Psocomorph group as in the dendrogram (fig. 104) more steps are added to the in-flight wing coupling mechanism series (figs. 92 through 97). The absence of this structure in Nanopsocetae is probably secondary. The lacinial tips and ovipositor valvulae also form rational series along this line.

It appears, therefore, that the Psocomorpha are phylogenetically included within the Amphientometae as a terminal monophyletic group. There are, however, some characters which suggest a contrary conclusion. For example, the rasp of the coxal organ is found in the Psocomorpha and Trogiomorpha but not in the Amphientometae or Nanopsocetae. This would be regarded as a new apomorphous development of the Psocomorpha in the theory developed above.

The relationship of the Nanopsocetae to the Trogiomorpha and the line bearing the Amphientometae and Psocomorpha still needs to be investigated. The Nanopsocetae and Amphientometae have been placed close together on the basis, in part, of plesiomorphous characters. However, it appears that the T-shaped sclerite of the subgenital plate, the tympanum of the posterior coxa, and ringing sculpture patterns of the antennal flagella, all characters absent in the Trogiomorpha and apparently absent in closely related orders, are here apomorphous and mark out a Nanopsocetae-Amphientometae line.

The electrentomoid families, then, bridge the gap between the Nanopsocetae and Amphientomidae. This accounts for why we find within this series of families forms very similar to the Nanopsocetae (*Musapsocus*, with lacinial tip of three tines and third valvula simple) and other forms very similar to the Amphientomidae (*Compsocus*, with lateral cusp of lacinial tip curved and bearing short, rounded denticles, third valvula deeply bilobed, compound eyes transversely color-banded). They arise precisely between the point on the line leading to Amphientomidae and Psocomorpha where the nodulus is acquired and the point where ctenidiobothria are acquired.

It must be noted that most of the species of the electrentomoid complex commonly share one apomorphous character: the junction of veins 1A and 2A in the forewing. This character is not universal, however, being absent in *Musapsocus huastecanus* and in *Manicapso-*

cus alettae. It occurs to very different extents in the different groups, and probably represents repeated parallel occurrences.

The families of electrentomoid psocids are arranged on the dendrogram (fig. 104) in order of appearance of various structures. The numbers in the internodes of the dendrogram refer to these structures listed in the explanation. The precise phylogenetic relationship between the Manicapsocidae and Compsocidae cannot be established with information now at hand. The two groups are apparently very close, and additional information may allow them to be united.

The fossil forms *Electrentomum* and *Parelectrentomum* are not yet well enough known to be placed with certainty in this scheme. They apparently belong either in the Manicapsocidae or Compsocidae, in one of the two possible positions indicated on the dendrogram.

The positions of the Troctopsocid genera within their family require explanation. At the first dichotomy, *Protroctopsocus* retains the apparently plesiomorphous traits of closed pterostigma, a row of spines on the anterior carina of the first femur (shared with Compsocidae, Amphientomidae, and some Psocomorpha), and 15 antennal segments (shared with Nanopsocetae, Manicapsocidae, and some Amphientomidae). It is specialized in form of the T-shaped sclerite and in possession of an m-cu crossvein in the forewing. At the next dichotomy, *Troctopsoculus* retains pretarsal claws alike, while its antennae are reduced to 11 segments. The remaining branch has pretarsal claws dissimilar while retaining 13 antennal segments.

Certain major changes in classification of the Psocoptera are called for by the phylogenetic scheme proposed above. For example, the Troctomorpha and Psocomorpha cannot be retained as taxa at the same heirarchic level. I believe that these ideas should receive the benefit of thoughts of other psocid investigators before such changes are proposed.

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Table I. Measurements (in mm.) and Ratios of Electrentomoid psocids.

	Forewing length	Posterior tib. length	Posterior t_1 length	Posterior t_2 length	Posterior t_3 length	$\frac{IO}{D}$	PO
Muscapsocus huastecanus, n.sp., ♂							
Sample Size	12	12	12	12	—	12	12
Minimum	2.09	0.81	0.34	0.13	—	0.87	0.66
Maximum	2.31	0.96	0.37	0.15	—	1.05	0.87
Mean	2.19	0.89	0.35	0.14	—	0.96	0.73
S.D.	0.068	0.038	0.010	0.007	—	0.047	0.05
Musapsocus huastecanus, n.sp., ♀							
Sample Size	13	13	13	13	—	13	13
Minimum	2.04	0.76	0.32	0.12	—	0.90	0.65
Maximum	2.31	0.89	0.36	0.15	—	1.14	0.87
Mean	2.15	0.85	0.34	0.14	—	1.02	0.73
S.D.	0.085	0.041	0.011	0.008	—	0.059	0.05
Musapsocus creole, n.sp., ♂							
Sample Size	6	6	6	6	—	6	6
Minimum	2.00	0.76	0.31	0.12	—	0.78	0.72
Maximum	2.15	0.83	0.36	0.13	—	0.91	0.80
Mean	2.08	0.79	0.34	0.13	—	0.86	0.76
S.D.	0.053	0.026	0.017	0.006	—	0.052	0.03
Musapsocus creole, n.sp., ♀							
Sample Size	10	10	10	10	—	10	10
Minimum	1.82	0.69	0.27	0.11	—	0.87	0.77
Maximum	2.09	0.81	0.35	0.14	—	1.02	0.88
Mean	1.96	0.77	0.32	0.12	—	0.96	0.81
S.D.	0.072	0.039	0.024	0.009	—	0.047	0.03

Table I. Measurements (in mm.) and Ratios of Electrentomoid psocids.

	Forewing length	Posterior tib. length	Posterior t_1 length	Posterior t_2 length	Posterior t_3 length	$\frac{IO}{D}$	PO
Musapsocus tabascensis, n.sp., ♂							
Sample size	4	4	4	4	—	4	4
Minimum	1.67	0.75	0.30	0.11	—	0.88	0.69
Maximum	1.89	0.77	0.33	0.13	—	0.92	0.78
Mean	0.79	0.76	0.31	0.12	—	0.90	0.74
S.D.	0.091	0.010	0.009	0.010	—	0.019	0.034
Musapsocus tabascensis, n.sp., ♀							
Two specimens	1.93	0.80	0.33	0.13	—	0.91	0.69
	1.78	0.71	0.33	0.13	—	0.94	0.73
Musapsocus birkenholzi, n.sp. ♂							
One specimen	1.89	0.83	0.31	0.13	—	0.91	0.69
Musapsocus simlae, n.sp., ♀							
One specimen	1.84	—	—	—	—	0.87	0.79
Protroctopsocus enigmaticus, n.sp., ♀ (brachypterous)							
Sample size	10	10	10	10	10	10	10
Minimum	1.98	0.94	0.45	0.08	0.09	2.00	0.55
Maximum	2.22	1.01	0.50	0.10	0.10	2.16	0.63
Mean	2.08	0.97	0.47	0.09	0.10	2.07	0.59
S.D.	0.082	0.023	0.016	0.004	0.004	0.063	0.022
Protroctopsocus enigmaticus, n.sp., ♀ (macropterous)							
Three specimens	3.26	0.99	0.49	0.09	0.10	2.05	0.55
	3.24	1.04	0.49	0.10	0.10	2.03	0.60
	3.49	1.06	0.50	0.09	0.10	2.03	0.60
Troctopsoculus morenus, n.sp., ♀							
One specimen	1.53	0.48	0.23	0.06	0.06	1.70	0.60
Troctopsocopsis martinicus, n.sp., ♂							
ample size	13	13	13	13	13	13	13
Minimum	1.38	0.48	0.20	0.04	0.05	1.31	0.57
Maximum	1.47	0.54	0.22	0.06	0.06	1.46	0.68
Mean	1.42	0.52	0.21	0.05	0.06	1.39	0.62
.D.	0.027	0.016	0.004	0.005	0.003	0.041	0.031
Troctopsocopsis martinicus, n.sp., ♀							
ample size	11	11	11	11	11	11	11
Minimum	1.33	0.47	0.19	0.05	0.05	1.36	0.57
Maximum	1.47	0.50	0.20	0.06	0.06	1.54	0.67
Mean	1.39	0.48	0.19	0.05	0.05	1.44	0.62
.D.	0.040	0.011	0.005	0.003	0.004	0.049	0.026

Table I. Measurements (in mm.) and Ratios of Electrentomoid psocids.

	Forewing length	Posterior tib. length	Posterior t_1 length	Posterior t_2 length	Posterior t_3 length	$\frac{IO}{D}$	PO
Troctopsocopsis intermedius, n.sp., ♂							
Two specimens	1.40	0.51	0.22	0.06	0.07	1.41	0.59
	1.38	0.50	0.21	0.06	0.06	1.34	0.50
Troctopsocopsis intermedius, n.sp., ♀							
Two specimens	1.35	0.49	0.21	0.06	0.06	1.50	0.63
	1.33	0.50	0.20	0.06	0.06	1.54	0.62
Troctopsocopsis luciensis, n.sp., ♂							
Sample size	9	9	9	9	9	9	9
Minimum	1.44	0.51	0.20	0.05	0.04	1.23	0.60
Maximum	1.79	0.56	0.23	0.06	0.06	1.43	0.66
Mean	1.49	0.54	0.21	0.06	0.06	1.37	0.63
S.D.	0.027	0.017	0.008	0.005	0.007	0.058	0.022
Troctopsocopsis luciensis, n.sp., ♀							
Sample size	10	10	10	10	10	9	9
Minimum	1.44	0.52	0.20	0.05	0.05	1.34	0.59
Maximum	1.53	0.53	0.22	0.07	0.06	1.49	0.68
Mean	1.48	0.53	0.21	0.06	0.06	1.43	0.64
S.D.	0.031	0.005	0.005	0.006	0.005	0.043	0.034
Troctopsocus separatus (Roesler), ♂							
One specimen	1.55	0.57	0.21	0.05	0.06	1.26	0.67
Troctopsocus separatus (Roesler), ♀							
Three specimens	1.55	0.57	0.21	0.05	0.07	—	—
	1.49	0.56	0.20	0.06	0.06	1.39	0.57
	1.58	0.54	0.20	0.06	0.07	1.52	0.57
Troctopsocus similis, n.sp., ♀							
Two specimens	1.84	0.65	0.24	0.06	0.07	1.50	0.65
	1.78	0.65	0.22	0.06	0.07	1.50	0.65
Troctopsocus bicolor, n.sp., ♂							
One specimen	1.55	0.57	0.21	0.05	0.06	1.26	0.67
Troctopsocus bicolor, n.sp., ♀							
Sample size	4	4	4	4	4	4	4
Minimum	1.89	0.62	0.23	0.06	0.07	1.41	0.52
Maximum	1.93	0.64	0.26	0.07	0.07	1.62	0.67
Mean	1.92	0.63	0.25	0.06	0.07	1.48	0.59
S.D.	0.019	0.010	0.015	0.005	0.002	0.093	0.060

Table I. Measurements (in mm.) and Ratios of Electrentomoid psocids.

	Forewing length	Posterior tib. length	Posterior t_1 length	Posterior t_2 length	Posterior t_3 length	$\frac{IO}{D}$	PO
	Epitroctes tuxtlarum, n.sp., ♂						
Three specimens	3.42	1.22	0.81	0.13	0.15	0.71	0.62
	3.33	1.16	0.76	0.13	0.16	0.78	0.56
	3.33	1.19	0.80	0.14	0.15	0.75	0.62
	Epitroctes tuxtlarum, n.sp., ♀						
One specimen	0.47	0.97	0.68	0.14	0.16	0.77	0.60
	Compsocus elegans Banks, ♂						
One specimen	2.22	—	—	—	—	1.02	0.72
	Compsocus elegans Banks, ♀						
Two specimens	2.42	0.85	0.52	0.10	0.10	1.08	0.42
	2.53	0.86	0.54	0.10	0.09	1.11	0.46
	Electrentomopsis variegatus, n.sp., ♂						
ample size	6	6	6	6	6	6	6
Minimum	2.91	0.92	0.86	0.09	0.12	0.78	0.62
Maximum	3.13	1.01	0.92	0.11	0.13	0.87	0.67
Mean	3.06	0.97	0.88	0.10	0.12	0.83	0.65
.D.	0.078	0.031	0.024	0.007	0.005	0.041	0.021
	Electrentomopsis variegatus, n. sp., ♀						
Three specimens	2.97	0.97	0.86	0.10	0.12	0.89	0.66
	2.89	0.95	0.84	0.11	0.13	0.84	0.62
	2.91	0.97	0.86	0.12	0.13	0.87	0.65

A NEW *PSEUDANOPHTHALMUS* FROM AN EPIGEAN ENVIRONMENT IN WEST VIRGINIA (COLEOPTERA: CARABIDAE)[1]

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Eyeless, rufotestaceous cave beetles of the genus *Pseudanophthalmus* (Trechini) are widespread in the Appalachian valley and Interior Low Plateaus (Barr, 1965; Jeannel, 1949; Valentine, 1945). Geographic isolation in different cave systems has led to an unusually large number of species, presumably the slightly modified descendants of edaphic ancestors which existed outside caves during the cold, wet climates of Pleistocene glacial maxima (Barr, 1965; Jeannel, 1949). Numerous species of other genera of trechine beetles, showing a more or less pronounced rudimentation of eyes and melanin pigments, are known from habitats other than caves, in mountainous glacial refugia of Europe and Japan (Jeannel, 1926-1930; Uéno and Baba, 1965). One species group of *Pseudanophthalmus* — not confined to caves but exhibiting similar reduction of eyes and pigment — inhabits humus and the upper soil strata at altitudes above 1000 meters in the Carpathians and Transylvanian Alps of eastern Europe (Barr, 1964). Blind, depigmented trechines have not been previously reported from Nearctic regions except in caves, although Barr (1965) recently commented: "It is conceivable that intensive collecting of endogenous carabids in the higher mountains of West Virginia and southwestern Virginia might reveal one or more surviving epigean populations of *Pseudanophthalmus*."

The purpose of this paper is to report the discovery of an eyeless, rufotestaceous, previously undescribed species of *Pseudanophthalmus* in an endogean habitat in the mountains of Pocahontas Co., West Virginia, and briefly to indicate its ecological and evolutionary significance. Three specimens were obtained from wet sand and gravel beneath medium-sized stones at the margin of a small brook on the east slope of Kennison Mountain, 28 April 1967. The locality is 7.2 kilometers NNE of Lobelia, in the Yew Mountains, Monongahela National Forest, about 300 meters west of the southwest corner of the Cranberry Glades, at an elevation of 1000 meters. Soil and

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water temperature was 8°-10° C. The stream flows over sandstones and shales throughout its short length, and in the area where the beetles were collected it traverses a second-growth, mixed hemlock and deciduous forest with an estimated gradient of 100 meters per kilometer. The nearest exposures of limestone and consequently the nearest known caves are in the vicinity of Lobelia and Hillsboro, 7 to 9 kilometers to the south, and the vicinity of Buckeye, 10 kilometers east. Troglomorphic collembolans — *Sinella hoffmani* Wray (det. K. Christiansen) — were found under the same stones with the beetles, and are here recorded for the first time outside of a cave.

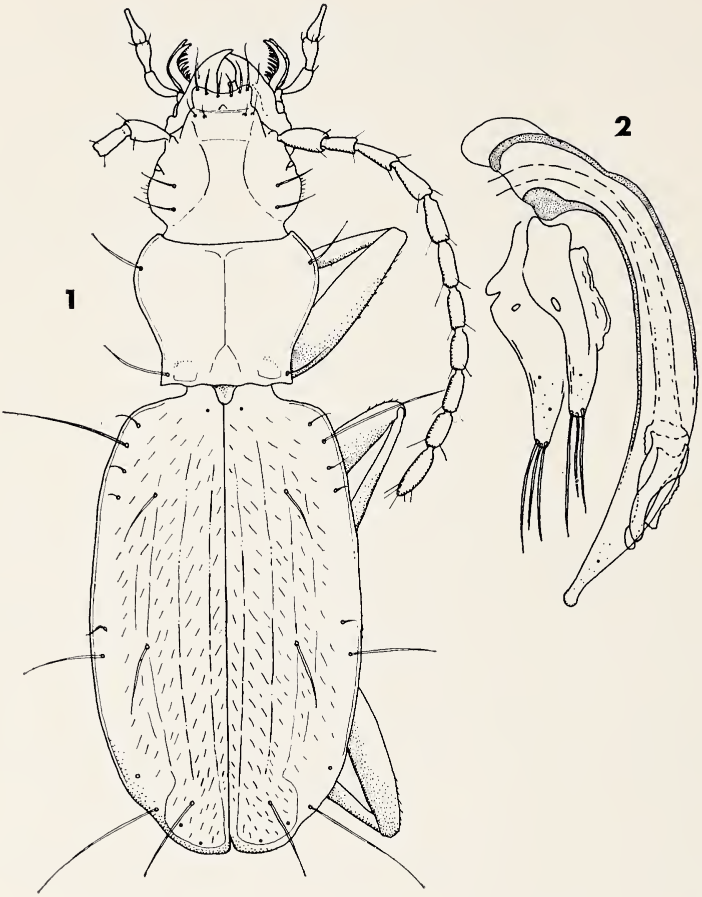
The possibility that the beetles were washed out of one of these caves, in the manner described by Barr and Peck (1965) for an Alabama cave *Pseudanophthalmus* sp., is easily excluded, since the caves are situated at elevations 250 to 300 meters lower than the Kennison Mountain locality, and are in different drainage basins. Furthermore, examination of more than 1000 specimens of *Pseudanophthalmus* spp. from caves of the Greenbrier valley has not revealed the presence of the species taken at Kennison Mountain. The occurrence of 3 specimens in close proximity to each other is additional evidence that the habitat is a normal one for the species.

The new species is most closely similar to *P. fuscus* Valentine (1931: p. 254), a species which inhabits caves of Pocahontas, Greenbrier, and Monroe counties, West Virginia, south of the Yew Mountains. It is readily differentiated, however, on the basis of the male genitalia and on other characters cited below. Although nominate *P. fuscus* shows no trace of an eye rudiment seen in the new species, undescribed subspecies of *P. fuscus* (or closely similar species) have a similar rudiment and the diagnosis must be made on the basis of other characters. *P. fuscus* is larger, more slender, and more densely pubescent, and the apex of its aedeagus is distinctively produced and more prominently knobbed.

Pseudanophthalmus sylvaticus Barr, new species

Figs. 1, 2

Closely similar to *P. fuscus* Val., differing in smaller size, less rounded head, the entirely glabrous pronotal disc, the more subdued anterior angles of the pronotum, the more rounded margins of the pronotum with shorter oblique portion and deeper antebasal sinuation, the more distinct longitudinal striae of the elytra, the less closely spaced humeral set of umbilicate punctures, the thicker and shorter segments of the antennae, and the shorter aedeagus without conspicuously produced and knobbed apex.



Figures 1 and 2. *Pseudanophthalmus sylvaticus* Barr, n. sp. 1. Female paratype, length 4.1 mm. 2. Aedeagus, male holotype, length 0.74 mm.

Length 4.08-4.12 mm. Form oblong, depressed. Rufotestaceous, shining. Dorsum of head and pronotal disc glabrous except for fixed setigerous punctures, elytra densely and finely pubescent. Microsculpture isodiametric on head, a very fine transverse meshwork on discs of pronotum and elytra. *Head* depressed, slightly transverse, conspicuously widest in basal third (widest at middle in *P. fuscus*); labrum evenly emarginate; eye rudiment present as a pale, lemon shaped areola 0.06 × 0.04 mm. *Pronotum* transversely cordiform, 1 1/4 times wider than long; width at apex 7/10 the maximum width, which occurs at apical fifth; base a little more than 9/10 as wide as apex; margins strongly rounded in apical half (in apical third in *P. fuscus*), then oblique, subparallel in basal sixth; hind angles prominent, right, sharp, and reflexed, the paramedian foveae deep; base feebly emarginate between hind angles. *Elytra* elongate-elliptic, length 1 3/5 times combined width; prehumeral borders slightly oblique to mid-line, humeri somewhat angular but rounded, humeral margins setose but not serrulate; disc with 5 or 6 irregular rows of pubescence on each interval; longitudinal striae broadly and very shallowly impressed (obsolescent in *P. fuscus*); distance between 1st and 4th umbilicate punctures 4/5 the distance between 4th and 5th punctures (3/5 in *P. fuscus*); anterior discal puncture at level of 4th umbilicate puncture, both anterior and posterior discals in 3rd stria; recurrent portion of apical groove short, rounded to subparallel, bending sharply inward to apex of 3rd stria at its anterior terminus; anterior apical puncture posteromedial to juncture of recurrent groove and 3rd stria. *Appendages:* antenna 5/11 the total body length, outer segments rather short and thick, 9th segment 3/5 as wide as long (1/3 in *P. fuscus*), densely pubescent; mentum tooth broad with apex emarginate; legs long and slender, but proportionately less slender than in *P. fuscus. Male* with secondary sex characters normal. *Aedeagus* 0.74 mm long (holotype) (0.88-0.90 mm in *P. fuscus*); basal bulb moderately expanded, with constriction before median lobe; apex gradually attenuate and very finely knobbed, not produced and conspicuously knobbed as in *P. fuscus*; parameres moderately elongate, with 3 apical setae; the middle one shortest; internal sac virtually unarmed, copulatory sclerites ± lobulate as in *P. fuscus* but shorter.

Holotype ♂ (United States National Museum) and 2 ♀♀ paratypes, east base of Kennison Mountain near the Cranberry Glades, elevation 1000 meters, Pocahontas Co., West Virginia, 28 April 1967 (T. C. Barr, leg.). Measurements of holotype: total length 4.12 mm, head 0.72 mm long × 0.74 mm wide, pronotum 0.72 mm long × 0.96 mm wide, elytra 2.22 mm long × 1.40 mm (combined) wide, antenna 2.32 mm long, aedeagus 0.74 mm long.

The discovery of *P. sylvaticus* strongly favors the hypothesis (Barr, 1965) that the ancestors of Nearctic cave trechines had already undergone much eye and pigment reduction and become edaphobites (obligate inhabitants of soil and humus) before colonizing caves. Under a periglacial climate, trechines would have been much more widely distributed than at present. Following retreat of the glaciers, these beetles would have become progressively restricted to sinkholes, cave entrances, deep ravines, and to higher forests where the climate remains cool and moist in summer. As regional climate became still warmer, they could have survived at lower altitudes only in caves, becoming troglobites (obligate cavernicoles) or at higher altitudes, becoming edaphobites in humus and the upper layers of the soil. In either case, ecological mobility would be greatly reduced, with concomitant restriction of gene flow, and many local endemics would have evolved.

In most parts of eastern United States the regional climate has apparently become too warm for continued survival of edaphic trechines. Unlike Europe, there are few high areas in eastern United States near the margins of Pleistocene glaciation to serve as refugia for cryophilic insects. In eastern West Virginia the combination of extensive cavern development in the Greenbrier valley and the existence of mountainous areas 1000 to 1400 meters high has preserved the edaphic, as well as the spelean remnants of the periglacial trechine fauna.

The occurrence of *P. sylvaticus* under rocks embedded in stream gravels is particularly interesting, since many similar small streams of the Greenbrier basin plunge from sandstone mountains into the limestone valley below and disappear into caves or sinkholes. Some species of *Pseudanophthalmus* are commonly found in nearly identical microhabitats along subterranean streams in caves. The logical sequence of events in cave colonization is thus obvious, at least in the Greenbrier valley. The eventual discovery of one or more American *Pseudanophthalmus* spp. which exist equally well in both the soil and in caves would not be surprising.

Cave colonization by trechines in eastern United States — particularly in areas adjacent to high, forested mountains and plateaus — may be somewhat more recent than commonly supposed. Much eye and pigment reduction may have taken place during adaptation to life in the soil of cool, moist forests. Eyespots are still present in *P. grandis* Val. (Greenbrier valley), in undescribed subspecies of *P. fuscus* Val. (Greenbrier valley), and in the species of the *petrunkevitchi* group of *Pseudanophthalmus* (Appalachian valley of Virginia; *petrunkevitchi* Val., *hoffmani* Barr, *hortulanus* Barr, *vicarius* Barr). It seems reasonable to suppose that the presence of these rudiments indicates more recent eye reduction than in completely eyeless species (all others in the genus). All of these species with eye rudiments inhabit caves in close proximity to mountains 1000 to 1300 meters high.

The current view of extrinsic isolation in different cave systems (Barr, 1965; Krekeler, 1959; see also Barr, in press) assumes that dispersal of troglobites from one system to another can take place only via subterranean routes, so that caves in limestone outcrops separated by non-caverniferous clastics (as in the Appalachian valley) are thought to represent habitats between which gene flow cannot take place. Once a species becomes a troglobite, its geographic distribution is controlled by its ability to disperse through subterranean channels and crevices, which are far more prevalent in soluble rocks than in clastics. It must be stressed that the discovery of *P. sylvaticus* does not basically change this view. For the moment, it appears that edaphic *Pseudanophthalmus* spp. in the United States are rare and probably restricted to cold mountain forests in a relatively few favorable places. Certainly the prevalence of such species needs further investigation.

On the other hand, the occurrence of *P. sylvaticus* supports the theory that cave *Pseudanophthalmus* spp. are relicts of rather widely distributed populations of edaphobites which existed near glacial margins and which colonized (and survived in) various cave systems during the early stages of interglacials. The peculiar occurrence of *P. illinoisensis* (Barr and Peck, 1966) in Hardin Co., Illinois, 175 kilometers west of all other known species of the *tenuis* group, which inhabit southern Indiana and adjacent Kentucky, is understandable in these terms. *P. illinoisensis* is so similar to *P. barberi* Jeannel, from the Pennyroyal Plateau of Kentucky between Mammoth Cave and the Ohio River, that the two species almost certainly share a close common ancestry, yet they are separated by the Ohio River and more than 150 kilometers of terrane underlain by sandstones, shales, and coals. A similar, though less spectacular case involving a pair of undescribed species of the *menetriesi* group in Tennessee and Kentucky is under study; a widespread, polytypic species inhabiting caves of the upper Cumberland and Green River drainages is separated from a closely similar form inhabiting a single cave near the center of the Central Basin.

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ATTACK BEHAVIOR OF DIGUETID SPIDERS AND THE ORIGIN OF PREY WRAPPING IN SPIDERS[1]

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Spiders use silk in prey capture in two ways: in the construction of webs which trap and partially immobilize prey, and in wrapping prey. Aerial webs have evolved independently in several families of spiders, including the Araneidae, Uloboridae, and Diguetidae (Kaston, 1966). As pointed out by Savory (1952, p. 20), a spider's web greatly extends the area covered by its sense of touch; it also at least partially immobilizes any prey which encounters it. Thus a web-living spider is more likely to "encounter" a new, partially subdued prey while handling another than is a webless spider. Most prey which become caught in a web will eventually work free and escape unless they are further immobilized. Barrows (1915) found that flies remained in the orbs of *Araneus sericatus (Epeira sclopetaria)* an average of only 5 seconds. However, most aerial web spinning spiders hang upside down in their webs, and if they dropped a prey which they had already caught while making a new attack, it would fall from the web and be lost. It is probably for this reason that many of these spiders wrap their prey and secure it to the web soon after encountering it, thus freeing their chelicerae for subsequent attacks.

Araneids and uloborids spin orb webs and use silk extensively to immobilize prey. Diguetids spin less highly organized webs, and never use silk in prey immobilization. However, they often apply silk to prey already subdued by biting. This paper shows how post-immobilization prey wrapping may have led to the use of silk as an attack weapon by the orb weavers.

I observed the following species attacking prey: *Aphonopelma sp.* (Theraphosidae, various ages, both sexes), *Metepeira labyrintha* (Hentz) (Araneidae, various ages, both sexes), *Argiope trifasciata* (Forskal) (Araneidae, females of various ages), *Uloborus diversus*

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(Marx) (Uloboridae, all ages, both sexes), *Diguetia canities* (McCook) (Diguetidae, mature females), and *Linyphia marginata* (Koch) (Linyphiidae, various ages, both sexes). While the behavior of spiders is often regarded as quite stereotyped, there was great variation in the details of attack sequences, even those exhibited by a single individual. However, the basic outlines of an attack were quite constant for the species observed, and, at least in one case, appear to be for an entire family (Uloboridae) (Marples, 1962, 1966). I have attempted to describe only these relatively fixed aspects of their behavior. Unless otherwise noted, the descriptions apply to attacks in well-lit situations on live prey at least 1/3 the size of the spider. Simpler attacks on smaller prey sometimes occur (especially in Araneidae).

Kaston (1966) surmises that the earliest spiders had no silk, and relied on speed and agility to capture their prey. The webless theraphosids, in the Mygalomorpha which is morphologically a primitive sub-order of spiders, used little more than this in their attacks. As also observed by Baerg (1959) and Gertsch (1949), they attacked by holding the prey with the tarsi of the legs and pulling it close to the mouth where it was bitten with the powerful chelicerae. The prey was overcome and held by the spider's chelicerae until their crushing action and poison immobilized it. Very little if any silk was used in the attacks. Occasionally, however, with the partially subdued prey held in the chelicerae, the spider arched its cephalothorax away from the ground and turned slowly in a circle, dabbing its spinnerets to the ground periodically. Possibly the silk laid during these actions served to give the spider a better grip on the substrate.

The attack behavior of the araneids and uloborids differed from that of the theraphosids. They spun orb webs and responded to the struggles of prey trapped in the web by running to it and quickly swathing it in silk. Araneids generally held the radius (or radii) on which the prey was resting with both legs II, straddling the prey as they wrapped it. Legs IV alternated in pulling swathing silk from the spinnerets and looping it over the prey. The spiral strands in which the prey was entangled were broken, and the band of swathing silk was wrapped onto the prey as it was spun rotisserie fashion by the palps and legs III and I. The spider bit the prey briefly with its chelicerae soon after the swathing began, and then delivered a longer bite after the prey was more completely wrapped. After the prey was completely covered with silk, the spider freed it from the web and attached a short line to it. Holding this line in tarsus IV, it carried the prey back to the hub of the web (or to its retreat) where it often wrapped the prey further. Then, as it turned to its normal head-down position, it attached the line from the prey bundle to the threads at this site, and began to feed, holding the prey with the palps and probably the chelicerae. If another prey landed on the web, the first prey was dropped, and hung by the short

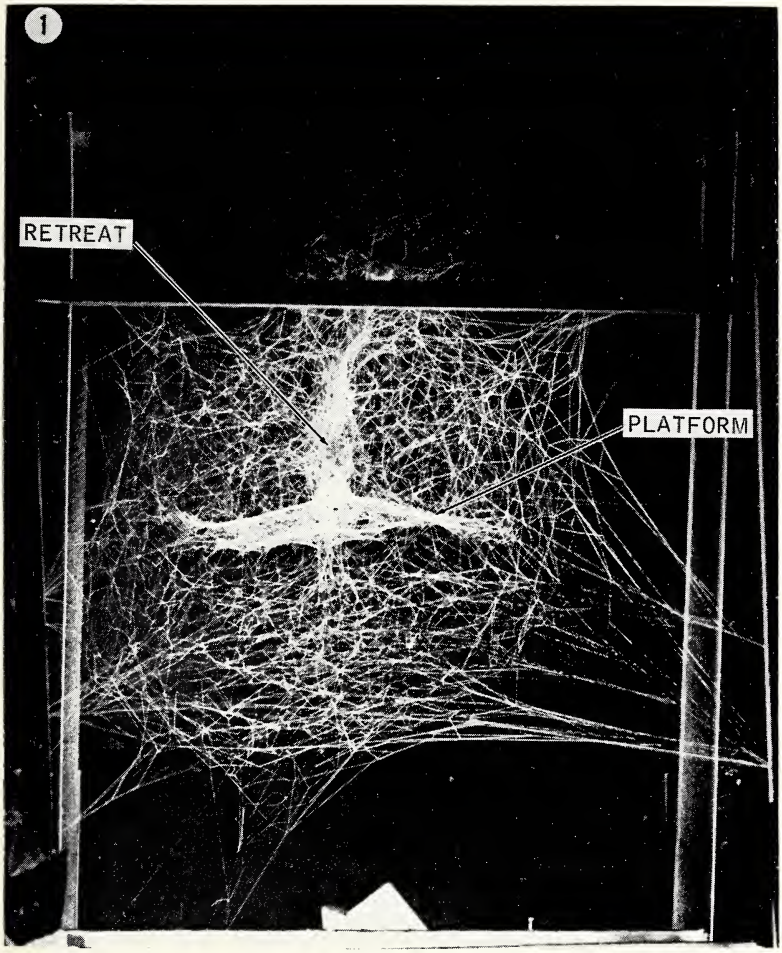

Figure 1. Web of mature female *Diguetia albolineata* built in a frame of wood and cardboard.

line as the spider rushed off to attack. This description agrees in all major points with those of Savory (1950) and Peters (1931, 1933).

The attacks by uloborids that I observed and that Marples reported (1962) were similar to those of the araneids with three major differences.

1. The prey was never bitten (Uloboridae have no poison glands). Immobilization was accomplished entirely by use of silk. This total reliance on silk represents the farthest departure of any spider from the primitive attack formula of "grasp and poison".

2. The prey was always carried in the palps and was never attached to the web. If another prey landed on the web the first was carried to the attack site, and often the two were wrapped into a single bundle. The presence of the first prey did not seem to hinder the movements of the second attack in any way.

3. Rather than straddling the prey at the start of an attack, the spider often turned to face away from it and pulled silk from the spinnerets, guiding it toward the prey with legs IV. In general, the larger the prey was, the farther the spider stayed from it as it commenced wrapping. The uloborids were thus farther from the struggling prey than the araneids in the initial stages of attack when the prey was least subdued.

The observations reported so far suggest this situation: *primitive — capturing prey with legs and chelicerae, holding it with the chelicerae and using poison to subdue it, not applying silk to it; advanced — capturing and subduing prey from a distance by applying silk to it, holding it with appendages other than the chelicerae.*

A clue to the origin of the use of silk in the evolution of attack behavior comes from the behavior of spiders in the poorly known family Diguetidae. These spiders spun relatively organized webs that were somewhat similar to those spun by linyphiids. The web was a roughly circular mesh platform suspended in a network of more widely spaced supporting strands. A nearly cylindrical "retreat" hung in the mesh just above the center of the platform (Fig. 1). The undersurface of the platform was continuous with the inside of the retreat. The spider remained inside the retreat during the day, and hung under the platform near the retreat at night.

When a prey fell onto the platform, the spider rushed out from the retreat and grappled with it.[2] If the prey was active (a moth for example), there was often a struggle lasting several seconds before the spider was able to grip it securely with the chelicerae, and the prey often escaped at this stage. Legs I were commonly thrust through the platform and their tarsi brought down on top of the prey, pressing it firmly against the platform and bringing it close to the chelicerae.

Biting and poisoning behavior was usually released only if the prey struggled. Only underfed spiders bit immobile prey. When a recently killed cockroach was dropped onto the platform, the spider rushed to it and grabbed it with legs I (and II?), but did not bite it. When the roach was pulled gently with forceps, the spider bit it. Objects which did not move within about 5 minutes of contact were pulled through the platform (see below) and dropped. Death-feigning insects may thus sometimes avoid capture.

Once the spider had a good grip with the chelicerae it held on until the prey's struggles subsided (usually about 10 minutes after the attack for prey about 1/2 the spider's size). If the prey was strong it sometimes pulled the spider around a bit before the poison took effect. All eight of the spider's legs were used to maintain its grip on the platform when this happened.

About five to ten minutes after the attack the spider slowly disengaged the prey (usually still twitching) from the web, pulling it through a slit in the platform made by breaking some strands and pushing others aside. Lines were cut by bringing them to the mouth region with tarsi III (and II?). Once when the prey was quite large in relation to the spider, the spider attached a line to the platform threads and then fixed this line to the prey before releasing its hold with the chelicerae to begin removing the prey from the web. This line anchored the prey more securely as the disengagement process began.

Often, especially when it was large, the prey got stuck as it came through the platform, and the spider tugged and pulled at it until it came free. Most, if not all, movements involved in freeing the prey from the web were accompanied by movements of the abdomen that caused the spider and the prey to bounce under the platform an estimated 5-10 times/sec as if it were an inverted trampoline. The function of these bouncing movements is not clear.

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[2] If the prey was entangled in the lines above the platform, the spider shook the web violently several times, sometimes causing the prey to fall onto the platform. If the prey did not fall, the spider sometimes climbed into the mesh to attack it there. The holes in the platform near the mouth of the retreat were occasionally used to gain access to the upper mesh, as Cazier and Mortenson (1962) supposed. Other times the spider climbed around the outer edge of the platform and into the upper mesh.

Holding the freed prey in its chelicerae, the spider carried it to the retreat, entered the mouth of the retreat, turned 180°, and began to eat facing downward. If another victim fell onto the platform the spider's first reaction was often to attach a line to the platform near the retreat. It then attached this line to the prey being eaten, and slowly rotated the prey so that several loops of thread were placed around it (almost everything diguetids do associated with spinning is quite slow and clumsy when compared with the orb

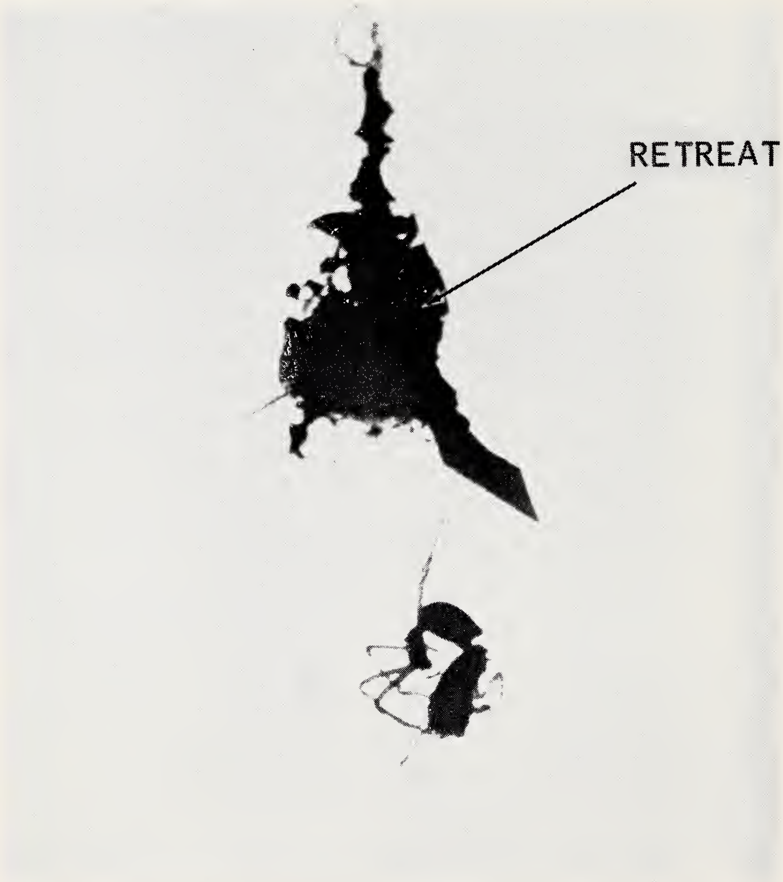

Figure 2. Mature female *Diguetia albolineata* wrapping a cockroach.

weavers' actions). The line was then attached to the prey and the platform again, and the spider left the prey dangling there as it rushed off to the second attack. Wrapping behavior often occurred just after the spider returned from an attack even in the absence of a second prey.

The actions involved in wrapping the prey were invariable, and to my knowledge, unique to the Diguetidae. The spider lowered itself until just the extended legs IV were holding the platform. With its abdomen bent at about 90° to its cephalothorax, the spider took the prey from its chelicerae and pressed it to its spinnerets with legs I, II, and III. It made one or more attachments to the prey, then rotated it slowly with these legs and laid a line around it. Additional attachments were sometimes made as the prey was turned. The number of turns was roughly dependent on the size of the prey and was usually between two and ten. Fig. 2 shows a *Diguetia albolineata* in the wrapping posture.

The aggressive use of silk by araneids and uloborids may be an elaboration of behavior like that of the diguetids. In the diguetids wrapping served only to anchor an already immobilized prey, whereas it was one of the chief means of immobilization for the orb weavers. The change from post-immobilization wrapping like that of the diguetids to uloborid-like immobilization wrapping would involve 1. wrapping at the site of capture, 2. wrapping the prey before it was immobilized by poison, and 3. applying greater quantities of silk to the prey. None of these steps involves elaborate behavior patterns not shown by the diguetids, and in fact under some conditions (large, strong prey) they will perform step 1.

The behavior of spiders in the family Linyphiidae gives another indication that the change from post immobilization to immobilization wrapping can occur easily. The linyphiids are allies of the Araneidae with web spinning and prey wrapping habits similar to those of the Diguetidae. They often applied a number of loops of silk to prey after it had been bitten, pulled through the web platform, and carried back to the center of the web. Their behavior differed from that of the diguetids in that they wrapped the prey much more often at the site of capture (always after biting it), and laid a longer line of silk onto the prey. Also, wrapping behavior was not as consistently released by the presence of another prey on the web. The first two differences indicate that silk is more of an offensive weapon for these linyphiids than for the diguetids. However, they apply less silk, and use it later in the attack sequence than the araneids, so their attack behavior is intermediate between that of the diguetids and that of the araneids.

The family Diguetidae is probably far from the evolutionary lines leading to the Araneidae and Uloboridae, but it is almost certain that some of the same selection pressures acted on animals in all of these lines as they became adapted to life in aerial webs. Thus it seems reasonable to suggest that the evolution of wrapping behavior in the orb weavers may have included steps similar to the behavior of the diguetids. This is not certain, however, as I have observed some spiders [*Hersalia sp.* (Hersiliidae), *Filistata arizonicus* (Filistatidae), and *Oecobius sp.* (Oecobiidae)] which perform immobilization wrapping and which live on (or near) the ground. The ancestors of the araneids and/or the uloborids may have had the ability to wrap prey even before they began to build aerial webs.

In summary, the steps from post immobilization wrapping to immobilization wrapping are not large, and intermediate behavior can be found. The elicitation of wrapping in diguetids by the presence of new prey in the web suggests that wrapping may have originated as a post-immobilization process designed to free the spider for new attacks, and only later devolved into a means of attack.

The possible stages of evolution of attack behavior, coupled with stages of web evolution (Kaston, 1966), are summarized below.

1. Prey is overcome by holding and biting, no trapping web is spun (Theraphosidae, Clubionidae, Salticidae, many others)
2. Low-lying trapping webs are built, prey are subdued by holding and biting (Agelenidae, Plectreuridae)
3. Aerial trapping webs are built, prey are overcome by holding and biting and are wrapped to prevent their loss during subsequent attacks (Diguetidae, Linyphiidae)
4. Aerial trapping webs are built, prey are overcome by biting and wrapping (Araneidae, Theridiidae)
5. Same as 4 except prey are overcome exclusively by wrapping (Uloboridae)

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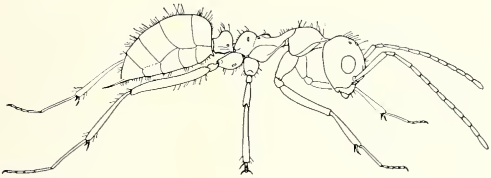

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PSYCHE

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TATUIDRIS, A REMARKABLE NEW GENUS OF FORMICIDAE (HYMENOPTERA)

By William L. Brown, Jr.[1] and Walter W. Kempf[2]

Introduction

The two remarkable ant specimens we describe below were sent to us originally by Mr. R. R. Snelling of the Los Angeles County Museum of Natural History in California. After prolonged study, we concluded that they represent a genus and species of Myrmicinae certainly very unlike any ants previously described, and that they could not reasonably be included in any living formicid tribe so far known. True, this new ant shares some striking habitus characters with certain Dacetini *(Glamyromyrmex, Gymnomyrmex)*, and also with the anomalous *Phalacromyrmex* (Kempf 1960), but analysis of these similarities indicates to us that they are mostly convergent and not based on close phylogenetic relationship.

In addition to comparisons with living ant genera, we checked through some likely fossil groups. Our attention soon came to rest on the primitive myrmicine genus *Agroecomyrmex,* of the Oligocene Baltic Amber (Wheeler 1914). We believe that our new genus and *Agroecomyrmex,* while at first sight very unlike each other, are nevertheless linked by some fundamental resemblances that we shall cite below in the tribal diagnosis and ensuing discussion. In fact, we feel that the two genera should be placed together in the same tribe. This tribe is already available in Carpenter's (1930) Agroecomyrmicini, raised to receive *Agroecomyrmex* and his then new

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[2] Provincialado dos Franciscanos, Caixa Postal 5.650, São Paulo, Brazil. Research supported by a fellowship from the Conselho Nacional de Pesquisas do Brasil.

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genus *Lithomyrmex* (later changed to *Eulithomyrmex*[3]) from the Miocene Florissant Shale of Colorado. The condition of the shale fossils is of course much inferior to that of amber specimens, and Carpenter was unable to make out some important characters of *Eulithomyrmex,* including the shape and position of the compound eyes, presence or absence of antennal scrobes, status of tibial spurs, etc. The venation of the queen wing, the broad head, and the form of the petiole, postpetiole and downturned gaster were enough, however, to make reasonable a placement of *Eulithomyrmex* in the same tribe as *Agroecomyrmex.* The diagnosis of the tribe offered below is based mainly on *Agroecomyrmex* and the new genus *Tatuidris,* but it is thought to agree with such characters of *Eulithomyrmex* as are known.

Tribe Agroecomyrmecini (emended)

Worker: Body short and compact, with hard, heavy integument, apparently capable of inrollment during lethisimulation. Head broad; eyes convex, set far back on the head, each at the posterior end of a well-marked, broad and deep antennal scrobe. Antennae robust, 7- or 12-segmented, with large apical segment. Mandibles robust, triangular. Clypeus broad, with transverse free margin. No ocelli. Alitrunk short and broad, but not as broad as head, convex above, dorsal sutures obliterated; propodeal declivity bounded by carinae with or without short teeth above. Petiole sessile, short and thick, with a prominent process beneath. Postpetiole short, deep and very broad, with the sternite well-developed; broadly attached to the first gastric segment, which is large and strongly downcurved. Remaining (apical) segments of gaster forming a cone directed downward or even anteriad. Legs robust, with slender simple tarsal claws; middle and hind tibiae each with a pectinate apical spur.

Female (not known for the new genus): Like worker, but winged and with the other usual caste differences. Forewing venation retaining all of Rsf2-3, though Mf2 is wholly contracted and lost.

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[3] By a very unusual coincidence, Clark (1928) had preceded Carpenter by a few months in the use of the name *Lithomyrmex* for a living genus of Australian ants, now considered to be a synonym of *Amblyopone.* Clark's paper, published in Western Australia, did not reach the United States for some time, but Carpenter (1935) eventually proposed *Eulithomyrmex* as the necessary substitute for his fossil genus.

Male unknown.

The tribe Agroecomyrmecini occupies a basal position in subfamily Myrmicinae, and in fact it may well represent the relicts of the primitive stock connecting the Myrmicinae to the ancestral tribe Ectatommini in subfamily Ponerinae, as already proposed by Brown (1954). Like *Myrmica* and allies among the lower Myrmicinae, the Agroecomyrmecini have pectinate spurs on the last two pairs of tibiae, but they are more primitive than *Myrmica* in the structure of the petiole, postpetiole and gaster. These characters recall the ectatommine genera *Gnamptogenys* and *Proceratium*, and the sculpture of *Agroecomyrmex* and *Eulithomyrmex* also matches that of various *Gnamptogenys* species-groups. The new genus *Tatuidris* is more specialized in its almost complete loss of sculpture, as it is also in other obvious ways.

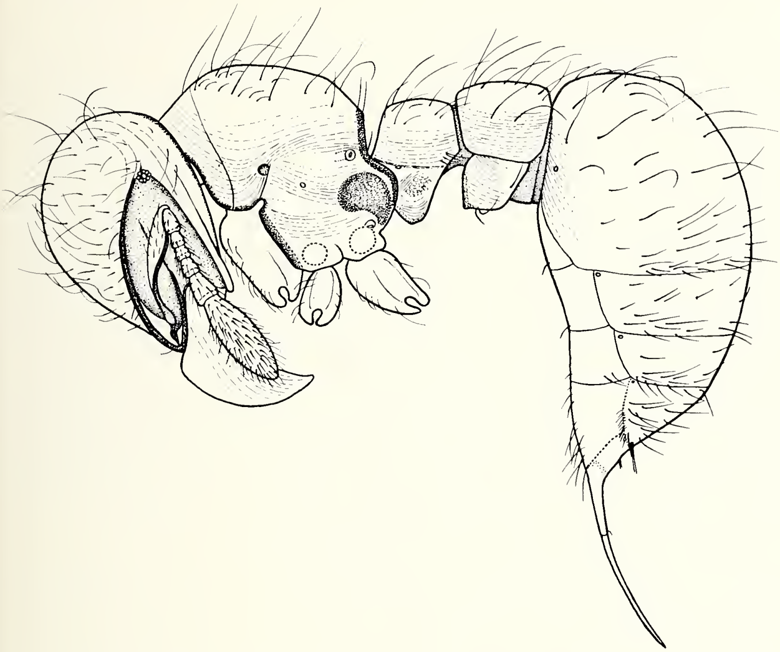

Figure 1. *Tatuidris tatusia* gen. et sp. nov., holotype worker in side view.

The new genus affords one case in a small but growing list of insect taxa found alive only after their other representatives had already been described as fossils. The Agroecomyrmecini are evi-

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dently a very old group, probably widespread during the early Tertiary in both hemispheres, and we may consider them as part of an early wave of the now dominant subfamily Myrmicinae that may have originated in an ectatommine stock near *Gnamptogenys*. We should expect the discovery from time to time of other fossil and living agroecomyrmecine relicts that will give us more details concerning the rise of the myrmicines.

Tatuidris, genus nov.

Worker: Size rather small, body exceedingly short and thickset. Head broad shield-shaped, narrowed in front and with strongly convex sides; convex dorsally and concave beneath; frontal carinae far apart, forming the lateral cephalic borders and the sharp upper margins of deep, long antennal scrobes. Eyes small, convex. Antennae 7-segmented, with a short, flattened-lamellate, apically broadened scape; funicular club indistinctly 2-segmented, the apical segment very large and thick. Clypeus broad, indistinctly bounded, transverse, with a sinuous, medially lamellate free margin. Mandibles heavy and robust, triangular, meeting along minutely crenulate but straight masticatory margins, each with two short, blunt teeth at apex and a massive brush of heavy setae along the inner (ventral) surface near the masticatory margin; each brush meshes with its opposite number at full closure (see Figure 3). Labrum broader than long, bilobed with a broad median excision. Maxillary palpi apparently 1-segmented; labial palpi 2-segmented.

Alitrunk remarkably short and broad, with continuously convex dorsum, forming an almost circular disc; humeri as seen in full dorsal view rounded, but vertically carinate on sides. Propodeal declivity concave, unarmed but bounded on each side by a carina; inferior propodeal plates rounded. Petiolar and postpetiolar nodes subrectangular as seen from above, the postpetiole a little wider behind than in front, its sternum large and deep, and with an anterior rim Gaster truncate in front as seen from directly above. Sting very long and strong.

Legs robust, femora and tibiae incrassate, tibiae obliquely terminated at apex, the extensor angle briefly produced and bearing a flat pencil of stiff, curved yellow setae; these are much larger on the forelegs than on the others. On the forelegs, tarsal segments 2, 3, 4 broadly triangular, with stout, darkened plantar setae; metatarsus with a dense brush of short yellowish setae occupying nearly the entire length of the flexor surface. On other legs, tarsal segments are mostly longer than broad.

Integument prevailingly smooth and shining, with fine, loose striation and reticulation mainly confined to the sides of the alitrunk, nodes and mandibles, and to the propodeal declivity. Pilosity fine, short to long, rather abundant. Color ferruginous.

Queen and male unknown.

Type and only known species is *Tatuidris tatusia* sp. nov., next described, from Central America.

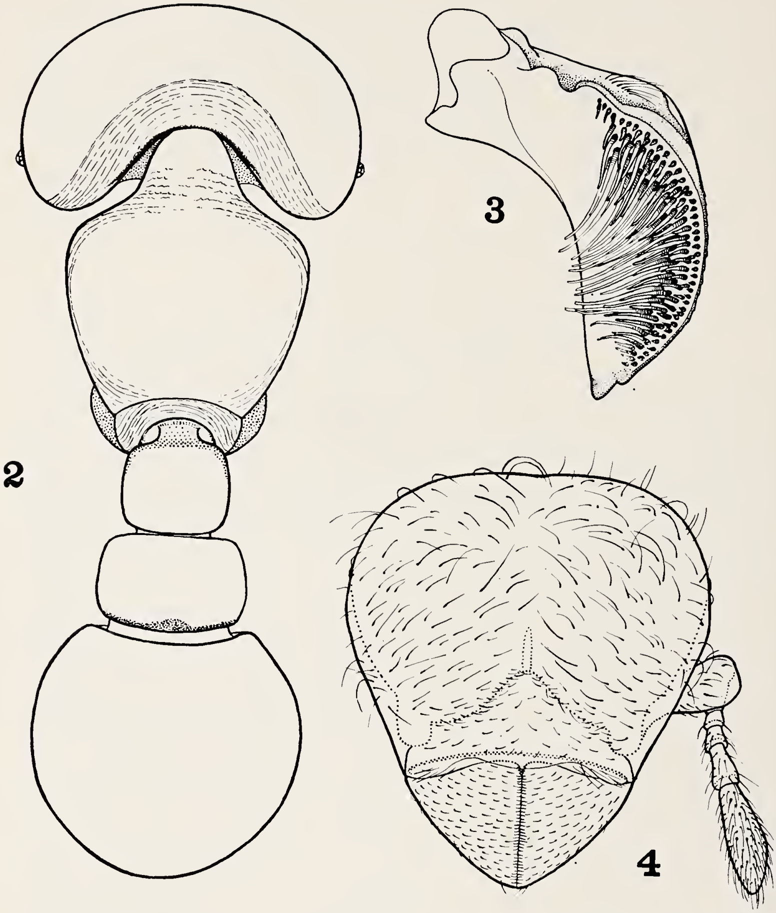
Tatuidris tatusia, species nov.

(Figures 1-4)

Holotype worker: Total outstretched length, including mandibles and axial dimension of gaster to its apex, 3.5 mm. Head L 0.82, head W 0.96, L closed mandibles 0.25, diagonal (Weber's) L of alitrunk (cervix omitted) 0.78 mm. Scape L (chord to basal collar) 0.40, L terminal antennal segment 0.30 mm, which is about half of total L of funiculus. Greatest diameter of eye 0.07 mm (about 10 facets total in each eye).

The form of the body, sculpture and pilosity are indicated in the figures. The clypeal suture is obsolete, marked only by a shallow sulcus in the middle, so the dotted lines in Figure 4 show only the approximate boundary. The free margin of the clypeus is concave overall, but an almost invisible, low, thin, transparent median lobe forms a median convexity in front of a darker, evenly concave internal line showing through the integument; this dark line is very prominent, and at first sight looks like the free margin proper.

The remarkable mandibular brush is shown in Figure 3; its constituent setae are thick, stiff and pigmented, short near the masticatory margin and becoming longer lateroventrad. In the closed mandibles, the brushes are visible only from ventral view. The trophi were dissected in both the holotype and paratype. The maxillary palpi were never clearly seen, but the parts assumed to represent them are extremely small and inconspicuous, albeit each with a long apical sensillum. The labial palpi consist each of 2 clavate segments with curved slender bases; the apical segment has a single apical sensillum. The foramen magnum is situated in a small funnel-shaped process extending rather prominently from the deeply excavated underside of the isolated cranium, but covered by the cervix in the entire insect. Pronotum marginate in front, but the margin becoming indis-



Figures 2-4. *Tatuidris tatusia* gen. et sp. nov., holotype and paratype workers. Fig. 2, holotype in dorsal view, pilosity omitted. Fig. 3, mandible of paratype, viewed from the midline looking laterad, to show the mandibular brush. Fig. 4, holotype, full-face view of head.

tinguishable from the sculpture in the middle, so not really seen in dorsal view (compare Figures 1 and 2).

The smooth parts of the integument bear very shallow indefinite indentations from which the setae arise, but these interfere scarcely at all with the generally polished surface. Delicately striate and reticulate areas are as shown on sides of the mandibles, posterolateral surface of head, front and sides of alitrunk, propodeal declivity and sides of nodes. Legs predominantly smooth and shining, with fine, rather long reclinate pilosity.

Color yellowish ferruginous, thick margins, etc. often appearing more brownish or blackish.

The single paratype worker is virtually identical with the holotype, but is a trifle larger (Head L 0.83, Head W 0.99, Weber's L of alitrunk 0.80 mm).

Holotype in Los Angeles County Museum of Natural History, Los Angeles, California; paratype in Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. Collected together 2 miles south of Quetzaltepec (Quezaltepeque), Prov. La Libertad, El Salvador, 17 July 1961, M. E. Irwin leg. The collection was made by Berlese funnel from humus, and the sample also contained specimens of a small *Solenopsis*, an undescribed species of *Eurhopalothrix*, and *Octostruma balzani*. Known only from the type collection.

The generic name comes from *Tatu*, the Tupi word and also the modern Brazilian word for the armadilloes, plus the Greek-based *idris*. *Tatusia* is another old generic name for an armadillo.

Though superficially *Tatuidris* bears some resemblance to species of the dacetine *Glamyromyrmex* complex of genera and to *Phalacromyrmex fugax*, it can be separated at once by means of its 7-segmented antennae, its brush-bearing mandibles, its toothless propodeum, the form and proportions of postpetiole and gaster, and by the presence of pectinate spurs on middle and hind tibiae, among other characters. It is very strongly isolated among living ant genera, though clearly a myrmicine. From the fossil genera of the same tribe, *Agroecomyrmex* and *Eulithomyrmex*, *Tatuidris* is readily distinguished by the shape of the head, 7-segmented antennae, lack of propodeal teeth, reduced sculpture, and also by the form and probably the armament of the mandibles.

It would be extremely interesting to know the food of *Tatuidris*; the mandibular brushes and powerful sting together suggest that the ant specializes in catching some active or slippery live arthropod prey in the soil or soil cover.

We acknowledge with thanks the aid of Mr. Roy R. Snelling who sent the specimens originally and generously allowed us to study and describe them. We are grateful also to the National Science Foundation for aid. The drawings are mainly the work of Mrs.

Margaret Menadue. We thank E. O. Wilson for critically reading the manuscript.

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NOTES ON THE BIOLOGY OF TWO CENTRAL AMERICAN *PTINUS* (COLEOPTERA: PTINIDAE) WITH A DESCRIPTION OF A NEW SPECIES

By Robin M. Andrews[1]

In this paper, a new species of *Ptinus* and the larva of *Ptinus latefasciatus* Gorham are described from Costa Rica. The larval habitat was discovered and comments will be made on the biology of the two species. The only species life history that has been recorded for New World Ptinidae is that by Linsley and MacSwain (1942) on *Ptinus californicus* Pic, a depredator in the nests of solitary bees, and there are host records for only a few other native species. Most of our knowledge of the family comes from the work of Europeans who have been concerned mainly with economically important species. Field work was conducted during participation in the Insect Ecology course given by the Organization For Tropical Studies in Costa Rica during February and March, 1967. The study locality was at Finca Taboga, near Cañas, Guanacaste Province. Specimens have been deposited in the collection of the Museum of Comparative Zoology [MCZ].

I would like to thank Dr. J. F. Lawrence, Dr. D. H. Janzen and Mr. Robert Matthews for the critical reading of this manuscript. I am grateful to Mr. R. D. Pope of the British Museum [BM] for the loan of specimens of *P. latefasciatus*.

Ptinus latefasciatus Gorham
(Figs. 1-11, 15, 16)

Ptinus latefasciatus Gorham, 1883: 194 (described from Vera Cruz, Mexico; Cerro Zunil, Paso Antonio, Dueñas, Guatemala; David, Tole, Panama); Pic, 1900: 256; Papp, 1962: 411. Syntypes in the British Museum.

Ptinus latefasciatus? var. *tripartitus* Pic, 1900: 256.

Ptinus mexicanus Pic, 1901: 299.

Description of adult: Sexual dimorphism absent. Patterned in black and reddish-brown; clothed with both black and gold setae;

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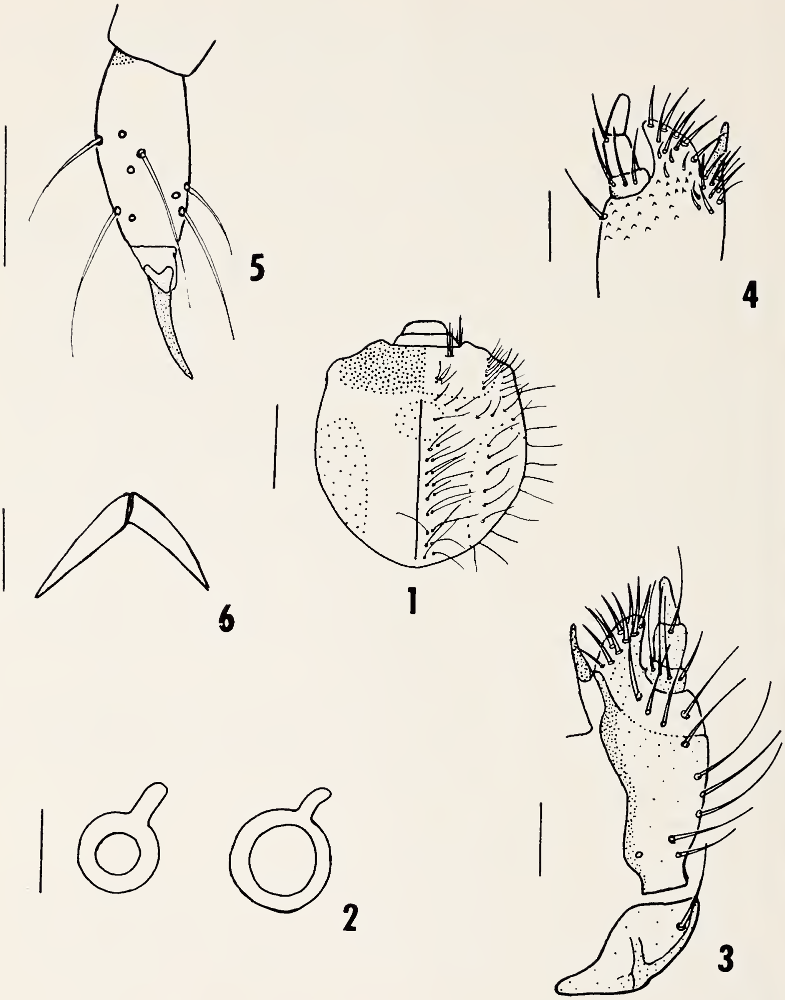


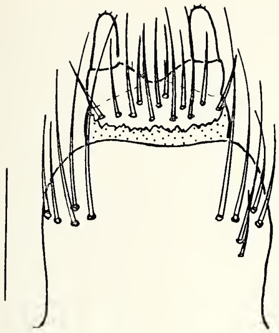
Larva of *Ptinus latefasciatus* Gorham

Fig. 1. Head capsule, dorsal view (scale .34 mm.). Fig. 2. Spiracles, right, thoracic spiracle, left, first abdominal (scale .04 mm). Fig. 3. Maxilla external view (scale .1 mm.). Fig. 4. Maxilla, internal view (scale .1 mm.). Fig. 5. Proleg, posterior view of left limb, setae of anterior side indicated by open circles (scale .1 mm.). Fig. 6. Preanal sclerite (scale .13 mm.).

elytra with large preapical and prebasal streaks of white recumbent hairs. *Total length:* 2.64-3.50 mm. *Greatest width* (across humeral callosities): 1.10-1.64 mm.

Redescribed from ♂ collected at Finca Toboga, 6 mi. S., 6 mi. W. Cañas, Guanacaste Prov., Costa Rica, Feb. 17, 1967, sweeping, river-bottom forest. *Total length:* 2.71 mm. *Greatest width* (across humeral callosities): 1.18 mm. *Head* with shallow vertical impression between eyes, vertex finely granulate, dull black; sparse recumbent white hairs and stiffer, more erect black setae on front between eyes. *Eyes* moderately large, projecting beyond maximum width of prothorax, situated laterally, just above base of mandibles, diameter of each eye two-thirds distance between eyes, occasional setae between facets. *Antennae* extending to middle of elytra, stout, with fine pubescence and with sparse black setae as long as each segment, middle segments each about 1.3 times as long as wide, basal segment twice as long as II, segments III-X slightly longer than II and subequal, ultimate segment 1.9 times as long as a middle segment. *Pronotum* with greatest width and length subequal, shiny black with basal half reddish-brown, anterior rim with long stiff black setae inclined posterad, anterior half coarsely granulate and strongly raised forming four gibbous areas, the central two not as distinctly separated from each other as they are from the lateral areas, clothed with stiff curved black setae that converge to a central point on each gibbosity, lateral and posterior sides of gibbosities with stiff golden setae, lateral gibbosities with a few white hairs preapically, posterior side of gibbosities with a median strip of short white hairs; lateral constrictions formed by deep vertical grooves that continue forward on each side between the lateral and central gibbosities as shallow, narrower grooves; basal half glabrous with a double row of setae at the basal edge, a deep median key-hole shaped groove extending to the raised area and slightly covered by a projection of this part. *Scutellum* U-shaped and covered with short white recumbent hairs. *Wings* fully developed. *Elytra* 1.65 times as long as wide, sides parallel, humeral callosities strongly developed and raised, diameter of punctures at middle of elytra about one-third as great as interspace width; area between preapical and prebasal streaks black, sutural margin, apices of elytra and basal area reddish-brown, black setae confined to black areas of elytra which are elsewhere clothed with golden setae; inclined setae of strial punctures extending slightly beyond next puncture; erect setae of intervals moderately short, setae of odd intervals only slightly longer than setae of even intervals; preapical streak of recumbent white hairs extending from second interval to lateral edge of elytra, short posterior prolongations into interval four and along elytral edge, a broad diffuse band of white recumbent hairs between the humeri, prebasal streak extending from interval two to elytral margin, a short prolongation into interval six, an additional diffuse patch of white hairs between the prebasal streak and the apices of the elytra. *Ventral surface* uniformly clothed in yellowish-gold hairs. *Abdomen* with sternites one to three somewhat connate mesally, sternite two twice as long as four. *Metacoxae* transverse, separated by one-half their width. *Legs* black, stout, covered with rather long and stiff golden setae, femora sprinkled with short white hairs, setae on upper tibia stiff and bristly, finer and inclined distally, tarsi with segments I to IV gradually decreasing in length, V equal to II and III combined. *Genitalia* (Figs. 15, 16) like typical *Ptinus* with ventral basal piece and lateral lobes attached dorsally to the median lobe. Median lobe gradually enlarged, widest just before apex, lateral lobes embracing closely the median lobe, basal piece 1.5 times as long as wide.

DESCRIPTION OF MATURE LARVAE: General body form as in other described ptinid larvae (Böving 1956, Manton 1945). *Total length:* 4-5 mm. *Head* (Fig. 1) hypognathous, pale yellowish-white, epicranial sulcus extending to the anterior third; three dorsal sclerotized areas: anterior third dark brown, small central patch and lateral areas yellowish-tan. Setae fine, white; four parallel rows on each side extending about midway from the rear edge, the two rows near the epicranial sulcus approximate, a single pair of setae in the central sclerotized area. Dark anterior area with two series of short setae marginally, four shorter setae near the midline, anteriorly an elongate pit with three to four setae, a second such structure with three setae on the anterior edge of the head at the lateral border of the anticlypeus, both with long setae projecting forward over the labrum. *Antennae* consisting of a sclerotized ring in a membranous socket located in the anterior edge of the head slightly above and mesal to the dorsal mandibular articulation. Tactile appendix of the antennae cone shaped, twice as long as wide, surrounded by several smaller sensory setulae. *Anticlypeus* rectangular, membranous. *Labrum* (Fig. 8) twice as wide as long, gradually curved distally; long setae born on the anterior edge and on either side basally, Y-shaped sclerites or tormae extending through the anticlypeus into the labrum; three basal labral sensillae: one on the midline and one between the arms of each torma. *Epipharynx* (Fig. 9) with four to six short



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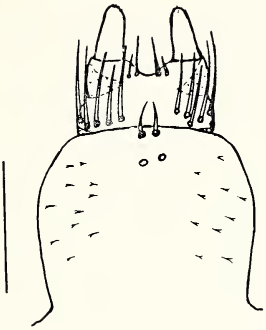

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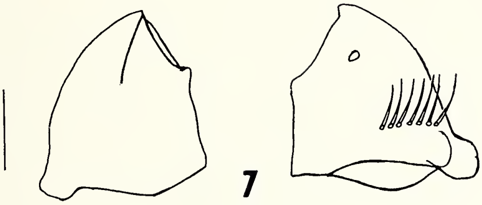

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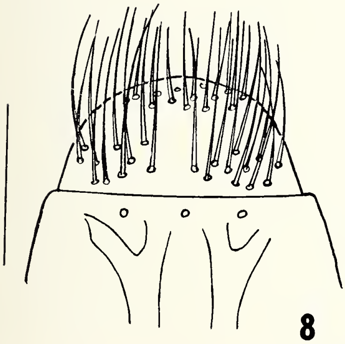

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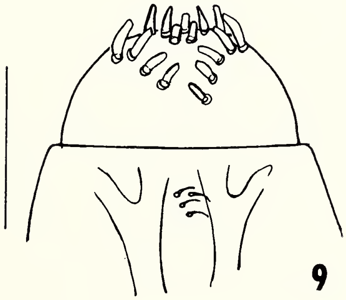

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Larva of *Ptinus latefasciatus* Gorham

Fig. 7. Mandibles, right, external view, left, internal view (scale .13 mm.). Fig. 8. Labrum, external surface (scale .1 mm.). Fig. 9. Epipharynx (scale .1 mm.). Fig. 10. Labium, internal view (scale .1 mm.). Fig. 11. Labium, external view (scale .1 mm).

blunt setae in each diverging row, similarly shaped setae on the anterior edge, and three or four short curved setae between the tormae. *Mandibles* (Fig. 7) slightly longer than greatest width, heavily sclerotized, dark brownish-black, with a single apical tooth; outer surface convex, with slight irregularities basally, a row of stiff setae paralleling the base, a somewhat elongate, mesal, preapical pit; inner surface convex, with a concave area mesally between apex and small acute tooth on the inner margin; inner margin compressed distal to the small tooth and more rounded proximal to it. *Maxilla* (Figs. 3, 4): cardo somewhat rhomboid, with one long setae on external distal surface; stipes two times as long as broad, with long setae on external lateral surface; palpus with three segments, the first short and broad, circled apically by about eight long setae, the second almost twice as long as the first, with two apical setae, the third subequal to the second, narrowed distally, apex with tiny sensory setulae; galea extending just beyond apex of second segment of the palpus, with numerous stout curved setae proximally; lacinia consisting of a well sclerotized spine, a number of short setae basally on the internal side. *Labium* (Figs. 10, 11): mentum large and fleshy, prementum smaller, about two-thirds width of the mentum; on the internal surface, mentum bearing numerous spicules laterally, two short stiff setae anteriorly and mesally, prementum with five or six setae on either side, two pairs of short setae projecting between the palps; on the external surface, the mentum with a group of about six long setae on either side, the prementum bordered basally by a sclerotized band, with numerous long setae anteriorly; labial palpus with two segments, the basal low and membranous with a small triangular sclerotized area on the internal surface, ultimate article longer than the first, apex with tiny sensory setulae. *Preanal sclerite* (Fig. 6) small, V or U-shaped, with arms asymetrically developed, enclosing only the very anterior end of the anal cushion. *Spiracles* (Fig. 2) annular with a single spout, thoracic spiracles 1.5

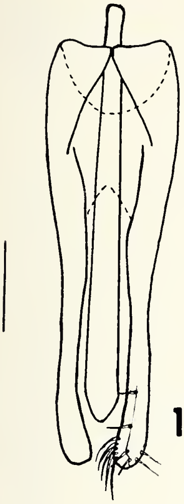
EXPLANATION OF PLATE 29

Ptinus costaricensis n. sp.

Fig. 12. Pronotum, dorsal view, stippling of surface structure and not indicating setation (scale .31 mm.). Fig. 13. Genitalia, holotype ♂, dorsal view, basal piece removed, setae indicated only for right lateral lobe (scale .13 mm.). Fig. 14. Genitalia, holotype ♂, ventral view (scale .13 mm.).

Ptinus latefasciatus Gorham

Fig. 15. Male genitalia, dorsal view, basal piece removed, setae indicated only for right lateral lobe (scale .13 mm.). Fig. 16. Male genitalia, ventral view (scale .13 mm.).



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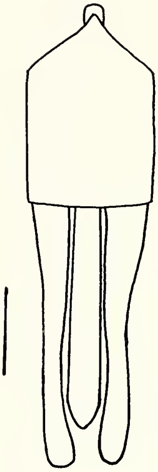

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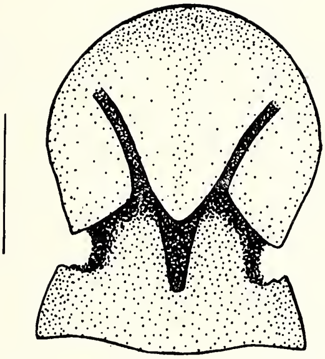

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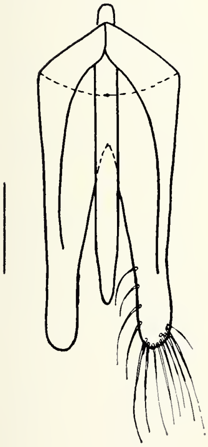

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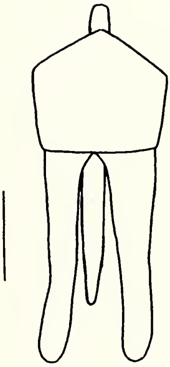

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ANDREWS — PTINUS

times as wide as the abdominal spiracles and with a less prominent spout. *Legs* (Fig. 5): proximal one-third of tibio-tarsus without setae, distal two-thirds with six to ten setae; pretarsus without setae, consisting of a soft basal portion and a long tapering claw, empodial lobe extending to basal fourth of the claw.

The nature and degree of variation is similar to that noted by Manton (1945) and Hall and Howe (1953), primarily differences in the numbers of setae and asymetry of certain parts. This variation was particularly noticeable in the mouthparts. Although the numbers of setae within groups or clusters vary between individuals, and from side to side on the same specimen, the placement of these groups appears to be invariable and probably is species' specific.

Although adults of two species were reared from the scats, the larvae are believed to be those of *Ptinus latefasciatus* because (1) this was the most numerous adult reared, eleven of this species to three of *P. costaricensis*, (2) pupae collected are *P. latefasciatus* by total length measurements (2.8-3.2 mm.) and (3) of the large size of the mature larva.

The larva of *Ptinus latefasciatus* can be distinguished from its North American congener, *P. californicus* (Böving, 1956), by numerous characters, some of which are listed in the following table.

Ptinus californicus	*Ptinus latefasciatus*
cardo with three setae	cardo with one setae
epipharynx with 1-3 setae in diverging rows	epipharynx with 4-6 setae in diverging rows
spiracle without spout	spiracle with spout
tibia with 16 setae	tibia with less than 10 setae
pretarsus with setae	pretarsus without setae

By the last mentioned character *P. latefasciatus* can be distinguished from *P. californicus* and all the species in Hall and Howe's larval key.

Distribution: Central America (Mexico, Guatemala, Costa Rica and Panama) and South America (Colombia, British Guiana and Brazil).

Material examined: costa rica: Guanacaste Prov., Taboga, 6 mi. S., 6 mi. W. Cañas, 10° 19′ N., 85° 09′ W., Feb. 15, 1967, collected from coati scats, 6 larvae. Same locality, Feb. 17, 1967, reared from coati scats, 11 adults. Same locality, Feb. 17, 1967. sweeping river-bottom forest, 4 adults. colombia: Rio Frio, Mgd., 2 specimens; Sta. Marta, Mgd., 1 specimen; Aracataca, Mgd., 5 specimens; Sevilla, Mgd., 1 specimen; Darlington collector [MCZ].

BRITISH GUIANA: Rio Essequibo (source), J. Ogilvie collector [MCZ]. GUATEMALA: Dueñas, G. C. Champion, B.C.A. Coll. III. (2)., Syn-type [BM].

Ptinus costaricensis, new species
(Figs. 12-14)

Holotype.— ♂, COSTA RICA: Guanacaste Prov., Taboga, 6 mi. S., 6 mi. W. Cañas, 10° 19′ N., 85° 09′ W., Feb. 17, 1967, reared from coati scats [MCZ, No. 31551]. Allotype, ♀, same date and locality, sweeping, river-bottom forest [MCZ].

Paratypes.— 2, same data as holotype [MCZ: 1]; 4, same locality as holotype, Feb. 15, 1967, sweeping, river-bottom forest [MCZ: 1].

DESCRIPTION: Sexual dimorphism absent. Reddish-brown, head and prothorax black with black extending into the anterior half of the elytra along the midline; clothed with gold setae; elytra with small preapical and prebasal streaks of white recumbent hairs. *Total length:* 1.90-2.65 mm. *Greatest width* (across humeral callosities): .78-1.15 mm.

Holotype ♂: *Total length:* 2.65 mm. *Greatest width* (across humeral callosities): 1.13 mm. *Head, eyes* and *antennae* as in *P. latefasciatus. Pronotum* (Fig. 12) shiny black, 1.2 times as long as wide, grooves and setation as in *P. latefasciatus* but without short white hairs on gibbosities. *Scutellum* and *wings* as in *P. latefasciatus. Elytra* 1.7 times as long as wide, sides parallel, humeral callosities strongly developed and raised; diameter of strial punctures at middle of elytra about 0.5 times as great as interspace width; inclined setae of strial punctures extending to next puncture, erect setae of interspaces longer than in *P. latefasciatus,* those of odd intervals 1.5 to 2 times longer than those of even intervals; recumbent white hairs of preapical streak extending from fourth to eighth interval, prebasal streak extending from the second to the fourth interval, and slightly posteriorly, from the fifth to the eighth interval. *Metasternum* clothed with intermingled gold and white hairs extending into the lateral areas of the metasternum. *Abdomen* and *metacoxae* as in *P. latefasciatus. Legs* reddish-brown, otherwise as in *P. latefasciatus. Genitalia* (Figs. 13, 14) relatively shorter than in *P. latefasciatus,* medium lobe narrowed at the apex, lateral lobes rounded apically, not closely approaching medium lobe, basal piece with length and width subequal.

This species is extremely similar to *P. latefasciatus* in proportions and in the structure of the pronotum. *P. costaricensis* is the smaller and more slender of the two species; there is little overlap of the gross measurements and the elytra and pronotum are relatively longer than in *P. latefasciatus*. Connation of the abdominal sternites is stronger in *P. costaricensis*. Superficially, *P. costaricensis* can be distinguished by it slighter coloration and smaller streaks of recumbent white hairs. The pronotal structure of these species is unique for New World *Ptinus* and separates these species from the *P. interruptus* group of Fall (1905), the species of which are patterned similarly to *P. latefasciatus*.

Biology

Ptinus costaricensis and *P. latefasciatus* were found to be breeding in coati *(Nasua narica)* scats. Coati troops were observed to use logs and large branches on the ground as part of their travel routes through the river-bottom forest along the Rio Higueron. Their feces, small flat cakes 5-6 cm. or less in diameter, were very numerous on these exposed surfaces. Many of the dry scats contained one to several larvae and pupae, and adults subsequently emerged from collected material. Naked pupae were in cavities in the scats; the larvae do not construct cocoons as has been noted for other ptinid species (Howe and Burgess, 1952).

Small dry deposits of fecal material may be the natural reservoir for many ptinid species as indicated by the few records for native species and some economic pests. Hinton (1941) summarizes the host data for British species, including nearly all of the economically important Ptinidae. The latter are known from a diverse assortment of dried organic materials, from stored cereals and grains to soiled clothing, bath sponges and opium cakes. Species that have successfully invaded the stored products habitat probably have come from several natural habitats, one of these being animal feces. For example, *Niptus hololeucus* Fald., a cosmopolitan pest in stored products, has been collected from rodent droppings (Hinton, 1941). Reddell (1966) has collected a new species of *Niptus* from raccoon scats in a Texas cave and several other species have been described by Brown (1959), also from caves and these may have similar habits. Ptinids recorded from bird nests (Linsley 1944, Woodroffe 1953) may also be associated with fecal material.

Adults of *P. latefasciatus* and *P. costaricensis* were commonly collected by sweeping understory vegetation of the river-bottom forest but were not taken in drier sites away from the river. As native ptinid species are rarely encountered by collectors, the occurrence of two common species at the study site may be attributed to peculiar climatic and biotic features of the area (Tropical Dry Forest, terminology of Holdridge, 1964). Collecting was done in mid-February, towards the end of the dry season (near Cañas, long and severe, Nov.-Apr., rainfall: 0-47.5 mm/mo, 1965 data, Anuario Meteorologico). There are several reasons why the dry season may be the most favorable period for breeding of these two species. (1) During this time their microhabitat, the coati scat, becomes dry and remains suitable for the feeding and development of the larva. Moisture and heavy rainfall would tend to wash apart exposed scats and result in rapid decomposition. (2) Because of the availability of water there, animal life becomes concentrated along rivers, especially so towards the end of the dry season. Coati scats are also concentrated in this localized area, thus augmenting ptinid breeding. It seems probable that during the rainy season (May-Oct., rainfall: 41-371 mm/mo) populations of these species would be much lower because scats would be dispersed over a wider area and suitably dry scats would be less common.

ADDENDUM: Subsequent to submitting this paper, I have had the opportunity to examine rainy season sweep samples from the study area. Neither *Ptinus latefasciatus* nor *P. costaricensis* was present in the extensive samples (800 sweeps in each area) from the river-bottom forest or immediately surrounding area. Dr. D. H. Janzen kindly provided access to sweep samples that he took on July 20, 1967, at Taboga, Costa Rica.

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TWO NEW SPECIES OF THE GENUS *OTIOTHOPS* (ARANEAE, PALPIMANIDAE) FROM THE VIRGIN ISLANDS*

By Arthur M. Chickering

Museum of Comparative Zoology

Otiothops walckenaeri MacLeay, 1839, was established on the basis of a female from Cuba. Miss Bryant recognized the male and very briefly described it in 1940. *O. oblongus* Simon, 1891 was described from a female taken on St. Vincent, B. W. I. The male remains unknown. I failed to collect any members of this family during my visit to this island in October 1966. *O. lutzi* Petrunkevitch, 1929, was also described from a female taken on Puerto Rico. The male has never been reported. I was again disappointed in not finding any members of this family during my period of collecting in Puerto Rico in January and February 1964. While collecting in Trinidad, W. I. in 1964 I found both sexes of a new species described as *O. carpenteri* Chickering, 1966. While collecting in the American and British Virgin Islands in July and August, 1966, I found specimens which seem to represent two additional species belonging to this very interesting genus. These are described in the following pages of this brief paper. As the matter now stands, six species of the genus *Otiothops* are now known from the West Indies. Two of these are known from both sexes, three are known only from females and the remaining species is known only from males. I think it safe to predict, however, that diligent searching in this region will yield several additional species.

Grant No. GB-5013 from the National Science Foundation made it possible for me to spend nearly four months collecting on nine West Indian islands in 1966 and is now helping me to continue my studies in the Museum of Comparative Zoology.

Types and all other specimens relating to the species described in this paper will be deposited in the Museum of Comparative Zoology, Harvard University.

Otiothops casobus sp. nov.

Figures 1-4

The name of the species is an arbitrary combination of letters.

Female holotype. Total length 6.08 mm. Carapace 2.73 mm

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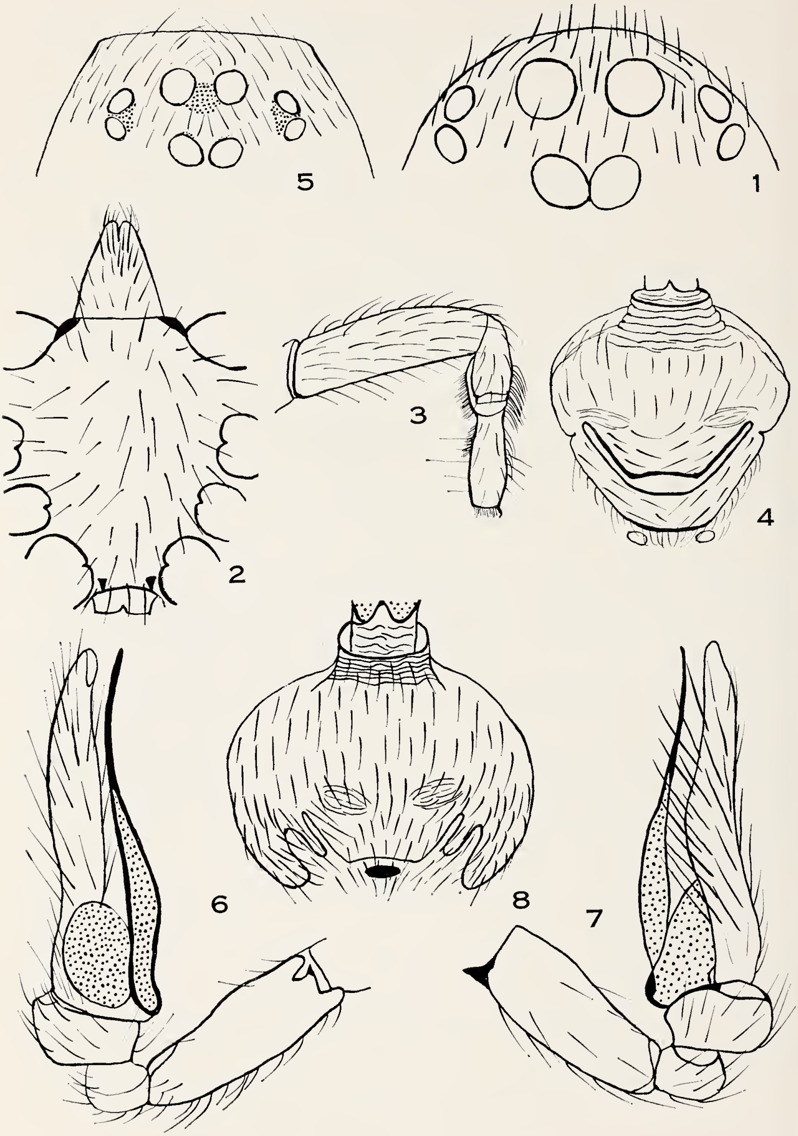

Chickering — Otiothops

long; 1.93 mm wide opposite interval between first and second coxae where it is widest; about 1.14 mm tall opposite interval between second and third coxae where it is tallest; height gradually increased from AME to beginning of posterior declivity the first half of which is very abrupt; thoracic fovea a fairly conspicuous pit near bottom of steep descent; surface finely granular and finely rugulose; anterior end bluntly rounded; posterior border squarely truncate. Eyes: eight in two rows; posterior row slightly longer than anterior row; viewed from above, anterior row gently recurved, posterior row strongly procurved thus bringing lateral eyes very close together (Fig. 1). AME circular, all others oval with irregularities in outlines. Ratio of eyes AME : ALE : PME : PLE = 14 : 13 : 15 : 11 (long axes used for measurements of oval eyes). AME dark; all others light with PME bright silvery. AME separated from one another by about 4/7 of their diameter, from ALE by about 5/7 of their diameter; PME in contact at posterior ends and obliquely placed; PME separated from PLE 7/5 of their diameter. Lateral eyes separated by nearly one third of the long axis of PLE. Central ocular quadrangle wider in front than behind in ratio of about 7 : 6; longer than wide in front in ratio of about 8 : 7. Height of clypeus equal to nearly three times the diameter of AME; clypeus deeply grooved just above ventral margin. Chelicerae, maxillae and lip typical of females of the genus. Sternum: typical of the genus; extended between all coxae; most widely extended between first and second coxae; terminated opposite fourth coxae where there is a pair of short tubercles (Fig. 2); fourth coxae separated by about 6/5 of their width; surface coarsely granulate. Legs: 4123 in order of length; tibial index of first leg 16, of fourth leg 11. First leg very robust with femur greatly elevated in proximal half; coxae 1423 in order of length and robustness; first metatarsus very short (Fig. 3); first tibiae, metatarsi and tarsi with iridescent ventroprolateral scopulae; all other metatarsi with distal, ventral scopulae; first patellae longest of the four; tarsal claws and claw tufts typical of the genus. Palp without a tarsal claw but with many tarsal bristles. Abdomen: typical of females of the genus; genital area

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EXPLANATION OF PLATE 30

Figs. 1-4. *Otiothops casobus* sp. nov. Fig. 1, eyes of female holotype from above; fig. 2, sternum and lip; fig. 3, first tibia, metatarsus and tarsus, retrolateral view; fig. 4, genital area, ventral view.

Figs. 5-8. *Otiothops pentucus* sp. nov. Fig. 5, eyes of male holotype from above; figs. 6-7, left palp, prolateral and retrolateral views, respectively; fig. 8, genital area, ventral view.

obscurely distinctive (Fig. 4); scutum continued to region shortly above the pedicel; with two short spinnerets partly surrounded by a narrow, chitinized wall. Color in alcohol: carapace, sternum, chelicerae and lip all a rich, reddish brown; other mouth parts and legs considerably lighter with variations among them; first pair of legs and maxillae darkest; abdomen with dorsum almost black; venter nearly the same with faint lighter dots; genital region and scutum like sternum.

Type locality. The female holotype and a single immature individual were taken on Virgin Gorda, British Virgin Islands, August 21, 1966.

Otiothops pentucus sp. nov.

Figures 5-8

The name of the species is an arbitrary combination of letters.

Male holotype. Total length 4.81 mm (cephalothorax and abdomen considerably separated). Carapace 2.05 mm long; 1.56 mm wide opposite second coxae where it is widest; .99 mm tall; nearly level along midline from PME to beginning of steep posterior declivity opposite second coxae; posterior declivity very steep through dorsal half and then more gradual to posterior border; with a conspicuous median pit at bottom of steepest part of declivity; surface finely granular; with a fairly well developed coat of procurved hair. Eyes: eight in two rows as usual; positions essentially as described for other species in this genus (1941, 1966). AME circular; all others oval with minor irregularities (Fig. 5). Ratio of eyes AME : ALE : PME : PLE = 12 : 10 : 11 : 8 (long axes used when eyes are not circular). AME separated from one another by about their radius, from ALE by about 2/3 of their diameter. Laterals separated by slightly less than 1/3 of the diameter of ALE. PME separated from one another by nearly 1/5 of their diameter, from PLE by a little more than 1.5 times their diameter. Central ocular quadrangle a little wider in front than behind and longer than wide in front in ratio of about 4 : 3. Height of clypeus equal to nearly three times the diameter of AME; ventral border grooved and with a narrow membranous margin. Chelicerae: typical of the genus; teeth and spines along fang groove essentially as described for *O. macleayi* Banks (1941). Maxillae typical of the genus. Lip: longer than wide in ratio of about 21 : 19; sternal suture line clear but, apparently, not permitting movement. Sternum: surface conspicuously granular but reduced along the central region; conspicuously extended between coxae in typical fashion; with the usual pair of small tubercles at posterior end. Legs: 1423 in order of length; tibial index of first leg 15, of fourth leg 12; scopulae as usual on first tibiae, metatarsi and tarsi and with considerable iridescence; small scopulae also on metatarsi 2-4; two claws and claw tufts as usual; trichobothria appear to be numerous on several segments. Palp: apparently quite distinctive; essential features shown in Figures 6-7. Abdomen: ovoid; only slightly flattened dorsoventrally; epigenital area with a well marked scutum reaching dorsally to surround the base of the abdomen (Fig. 8); two spinnerets as usual, with a narrow chitinous wall nearly surrounding spinnerets and anal tubercle.

Type locality. Male holotype, one male paratype and an immature specimen were taken on St. John, U. S. Virgin Islands on July 22, 1966. Two immature specimens previously assigned to *O. lutzi* Petrunkevitch (Chickering, 1966) are now placed in this new species.

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NOTES ON NEOTROPICAL TABANIDAE (DIPTERA). XI. *STENOTABANUS STARYI* N. SP. FROM CUBA*

By G. B. Fairchild

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In 1923 Brunetti described *Silvius punctipennis* from 3 specimens from Sierra Maestra (Oriente Prov.) Cuba. Bequaert (1940) transferred the species to *Tabanus (Stenotabanus)*, renaming it *brunettii* due to pre-occupancy by *Tabanus punctipennis* Macquart 1838. Bequaert (1940) included specimens from Hispaniola and Puerto Rico, as well as Cuban material in the species, and noted the great variability in size, from 6 to 12 mm. Brunetti gives 7 to 7.5 mm., though Bequaert states that the paratype in Deutsches Entomologisches Institut measured 9.5 mm. He did not study the holotype in the British Museum. Mr. Harold Oldroyd, at my request, very kindly measured the holotype and paratype in B.M. He found the holotype to measure 10 mm. in wing length, 8 mm. in body length; the paratype 8 mm and 8 mm.

Recent extensive series collected in Cuba by P. Stary and kindly sent to me for study by Dr. Milan Chvala, indicate that two very closely similar species appear to be present. The larger of these, with wing lengths from 7.7 to 10.4 mm. (58 specimens measured) is *brunettii* Beq. as shown by measurements of the types. The smaller species, described below, has wing measurements of 5.2 to 6.5 mm. (17 specimens measured), so that there is a gap of over 1 mm. in wing length between the two populations. The means and medians of these measurements for the two species are 5.3 and 5.85 for the small species, 8.2 and 9.0 mm for *brunettii*. These dimensions are correlated with slight differences in color and wing pattern. Both species occur together in many localities, though *brunettii* appears dominant at higher elevations.

The status of the forms found on Hispaniola and Puerto Rico will need long series for clarification. The few specimens available are rather intermediate in size between the two Cuban forms, but slightly different in wing pattern from either and from each other. Whether they are geographical races (subspecies) of one or the other of the Cuban forms, or best separated on a specific level cannot be

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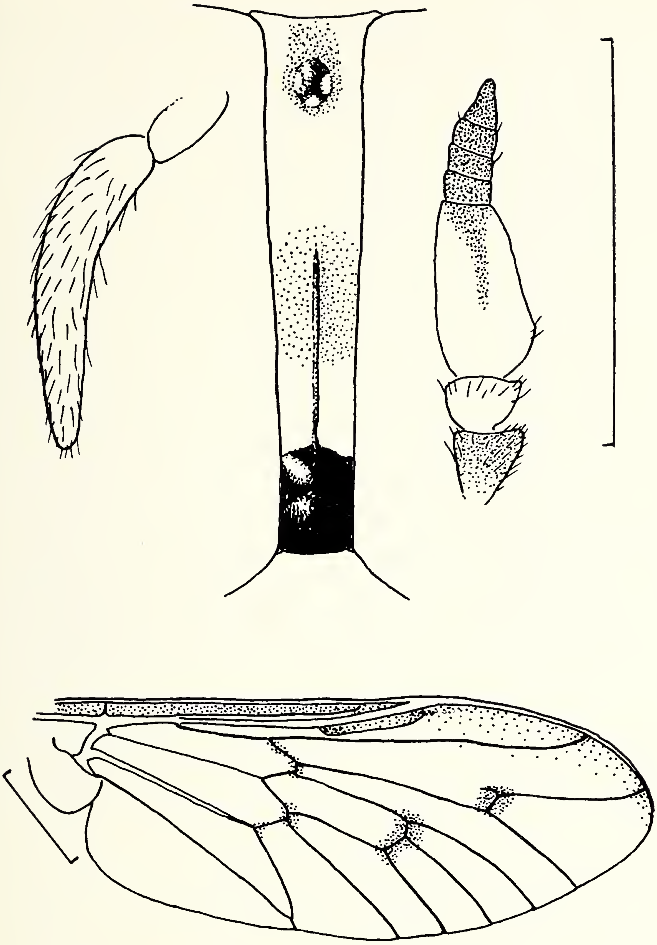

Fig. 1. *Stenotabanus staryi* n. sp., palpus, frons and antenna, holotype. Wing, paratype. The scale lines represent 1 mm.

decided on the basis of the meagre material available to me (2 from Hispaniola, 1 from Puerto Rico).

Stenotabanus staryi n. sp.

Female. Length 6.8 mm., of wing 6.1 mm. Eyes bare, purple with 2 green transverse bands, the upper narrower than the lower. Frons 6.8 times as high as basal width, slightly wider at vertex, as figured, clothed with steel grey pollinosity which shows a median ill-defined blackish area in middle of frons in certain lights. Tubercle at vertex with clear vestiges of ocelli, surrounded by a semi-bare area thinly clothed with dark pollinosity. Callus and median ridge black, shiny. Subcallus pollinose, slightly yellowish tinged, and at sides somewhat more brownish. Fronto-clypeus and genae steel grey pollinose, the sparse beard whitish. Antennae as figured, the first segment dark brown, thinly pollinose, black-haired; second segment orange, black-haired; third segment reddish orange on basal two-thirds of basal plate, the apex blackish, with an ill-defined blackish streak in middle; style black. Palpi as figured, dull yellowish in ground color, whitish pollinose, and clothed with sparse long brassy hairs basally, shorter black hairs on apical two-thirds. Proboscis slightly longer than palpi, the labella large, soft, pollinose, blackish.

Mesonotum blackish-brown in ground color, grey pruinose anteriorly and with a pair of grey pruinose dorsolateral stripes. Notopleural lobes and area around wing bases slightly paler. Vestiture sparse, of short pale hairs. Scutellum concolorous, its posterior border with paler pruinosity. Pleura paler, brownish, pale pollinose and largely pale-haired. Coxae and femora blackish in ground color, pale pollinose and sparsely pale-haired. Fore tibiae yellowish on basal half, blackish distally, remaining femora yellowish, sparsely pale-haired basally, dark-haired apically. No hind tibial fringe. Fore tarsi black, remainder yellow basally, the terminal segments dusky. Halteres with pale stem, knob largely blackish, except extreme apex paler. Wings as figured, the costal cell dark yellow, clouds brown. Basicosta without macrotrichiae, acutely pointed. Costa without basal groove.

Abdomen blackish-brown in ground color, the posterior borders of all tergites, except seventh, broadly whitish. First and second tergites slightly paler at sides. Pollinosity thin, dark on dark areas, yellowish white on pale hind borders. In addition, sides of first and second tergites, and faint broad median triangles are grey pollinose. Hairs are sparse, but reflect the underlying colors, dark on dark areas, yellowish on pale areas, including the indefinite median triangles. Beneath the abdomen is paler, with less contrast in basal colors, wholly pale pollinose and pale haired.

Holotype ♀ Cuba, Sierra Maestra, Pico Turquino, Oriente, 14-8-1965, P. Stary coll. To be deposited in M.C.Z.

Paratypes, 3 ♀ Sierra Cristal, Cayo Verde, 20-8-1965, P. Stary; 4 ♀, Cupeyal, Oriente, 23-3-1965, P. Stary; 3 ♀ Cupeyal, sev., od

Guantanamo, 22-3-1965, P. Stary; 1 ♀, Sierra Maestra, Oriente, Santa Ana, 28-5-1965, P. Stary; 1 ♀, coast below Pico Turquino, eastern Oriente, July 26-30, 1936, P. J. Darlington; 1 ♀, Yunque de Baracoa, Oriente, July 13, 1936, 1000-1800 ft., Darlington; 2 ♀, Mts. n. of Imias, Eastern Oriente, July 25-28, 1936, 3000-4000 ft., Darlington; 1 ♀, Soledad, Sta. Clara, Cuba, VII-2-1932, Bates and Fairchild. To be deposited in Museum of Comparative Zoology, Harvard University, Narodni Museum, Prague, and coll. C. B. Philip.

The Stary specimens are mostly somewhat grease darkened and a number are lacking appendages, apparently taken by hand. The remaining material is generally paler, the abdomens more brownish and thoraxes more clearly striped.

Aside from smaller size, this species differs from *brunettii* in smaller wing spots, less clearly marked median abdominal triangles, stubbier antennae which are generally more extensively yellow or orange, and in proportionally wider pale abdominal bands. The wings are always slightly shorter than body, while in *brunettii* they are always slightly longer than body.

Dr. Stary also collected 88 specimens of *St. brunettii* from Pico Turquino, Santa Ana, Loma de Cordero, Cabezal de Palma M. and Pico de Cuba, all in Oriente Province. I have also seen material from other localities in Oriente Province and from Buenos Aires, Trinidad Mts., Santa Clara in M.C.Z. Those from the latter locality are smaller and paler.

Bequaert's action (1940) in renaming *Silvius punctipennis* Brunetti arose from his belief that *Stenotabanus* was no more than a subgenus of *Tabanus*, so that *punctipennis* Brunetti 1923 became a junior secondary homonym of *Tabanus punctipennis* Macq. 1836, upon transfer by Bequaert to *Tabanus (Stenotabanus)*. But since this action was taken before 1960, it is my belief that strict application of Article 59c of the International Rules of Zoological Nomenclature requires the retention of *brunettii* Bequaert 1940. This article states that names of this sort published after 1960 are to be changed, and by implication, that those proposed before that date are to stand.

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BIOCHEMICAL DIFFERENTIATION OF THE SIBLING BLACK WIDOW SPIDERS, *LATRODECTUS MACTANS* AND *L. VARIOLUS**

By John D. McCrone

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A recent revision of the black widow genus *Latrodectus* published by Levi (1959) has stimulated a great deal of interest in this medically important group of spiders and has served as the basis for several subsequent investigations in various parts of the world (Abalos, 1962; McCrone and Levi, 1964; Szlep, 1965; Levi, 1966). All of these have shown that several species which are virtually indistinguishable morphologically can readily be separated on the basis of various aspects of their biology. These findings in turn have led students of the group to seek additional taxonomic characters for use in the separation of these species.

Rabaey and Verriest (1958) after a survey of the comparative agar gel microelectrophoretic patterns of the hemolymphs of 33 species of spiders, exclusive of any *Latrodectus* species, concluded such patterns could be very useful for the differentiation of species, particularly those within the same genus. Encouraged by their results, I decided to determine whether a technique of this type would provide useful taxonomic information in the genus *Latrodectus*.

This investigation was supported by Public Health Service Research Grant GM11206 from the National Institute of General Medical Sciences. I wish to thank Miss Marietta Marra and Mr. Paul Dell for their technical assistance.

Materials and Methods

An increasing number of electrophoretic techniques have become available in recent years including agar, starch, disc and vertical acrylamide gel electrophoresis. All of the latter have been used to some extent in evolutionary and taxonomic studies (Manwell and Baker, 1963; Hubby, 1963; Hubby and Throckmorton, 1965; Coates, 1967) and have given satisfactory results. I have found, as did Hubby (1965), that the vertical acrylamide gel technique gives particularly good results. The acrylamide gel slab is much easier to handle than the starch gel and there is comparable resolution. Disc

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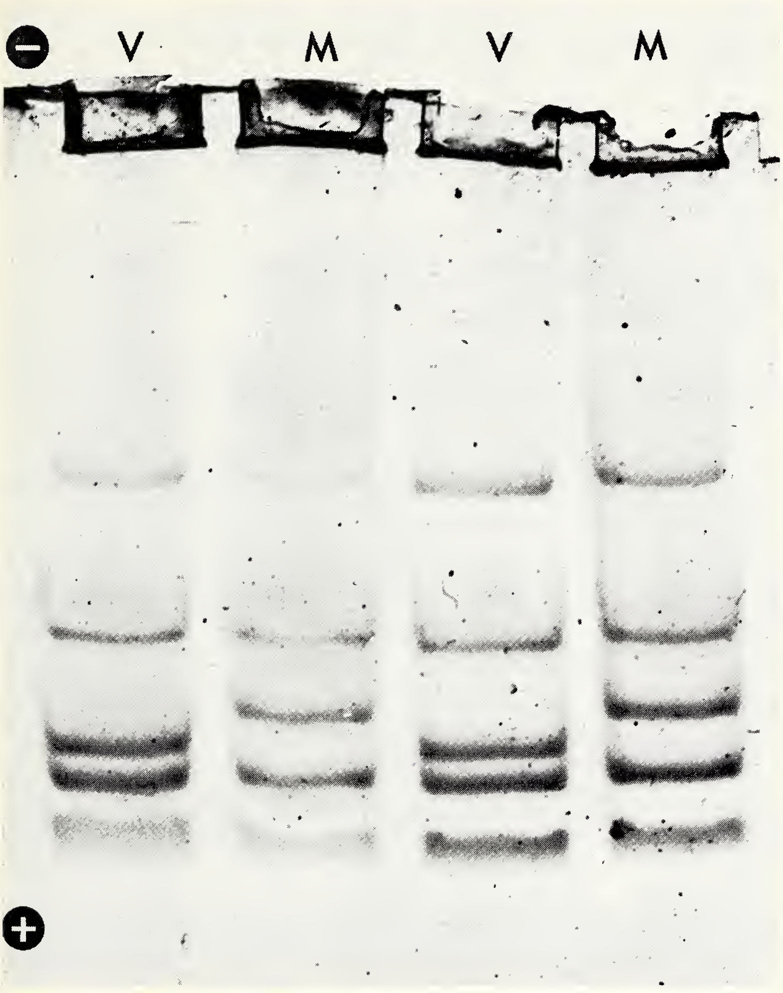

Figure 1. Vertical acrylamide gel electrophoretic patterns of the hemolymph proteins of female *Latrodectus mactans* (M) and *L. variolus* (V).

electrophoresis also gives excellent resolution but is less useful for taxonomic comparisons because it is difficult to run standard reference proteins as controls in the same gels as the samples. In the case of *Latrodectus* hemolymph there is the additional advantage that the hemolymph from a single spider will form a distinct pattern in a single slot when the 8-slot slab is used. This allows a determination of the amount of variability between the patterns of individual spiders.

The spiders used in this study were mature females of the sibling species *Latrodectus mactans* (Fabricius) and *Latrodectus variolus* Walckenaer collected in Florida during the summer at St. Petersburg and Torreya Ravine State Park respectively. These females are very difficult to separate using conventional morphological criteria.

Hemolymph was obtained from individual spiders by severing the legs at the junction of the coxa and trochanter and then drawing up the expressed hemolymph into a polyethylene capillary tube connected to a 1 cc hypodermic syringe. The hemolymph was then mixed with 0.05 ml of a Karo syrup — buffer solution (9 parts Tris buffer pH 9.0: 1 part Karo syrup). The Karo increased the density of the solution making it easier to layer the sample into the gel shots.

The electrophoretic runs were carried out in a cell manufactured by the E-C Apparatus Corp. in which a 8-slot, 8 per cent acrylamide gel slab was used. The hemolymph sample from each spider was loaded into one of 6 slots, the other 2 slots were loaded with 0.1 ml of a solution of human serum albumin (0.05 mg/ml). The albumin solution was lightly stained with bromthymol blue so that its migration could be followed. Tris buffer (pH 9.0) was used in the buffer compartments of the cell and 150 ma (560-780V) was applied for 90 min. The gel slab was then stained with amido schwarz and the relative mobility of each of the hemolymph protein fractions was obtained by comparing its mobility to that of the human serum albumin.

Results

The individual electrophoretic patterns of the hemolymph proteins of 10 *L. mactans* and 11 *L. variolus* females were recorded. Five fractions were found in each species and the average relative mobility of each of these fractions is given in Table I. Each fraction is numbered relative to its position from the origin, fraction 1 being the closest to the origin. Figure 1 shows the characteristic patterns of the two species. All were run in the same gel. There are no significant differences in the average relative mobilities of fractions 1, 2, 4 and 5 in the two species, but there is a clear cut difference in those of fraction 3. The magnitude of the difference is such that the relative mobility of this fraction can be used to separate all tested females of the two species.

TABLE I

Relative Mobilities of the Protein Fractions of the
Hemolymphs of Female *Latrodectus mactans* and *L. variolus*

Species	No. of Individuals	Fraction No.				
		1	2	3	4	5
L. macans	10	0.484 ± 0.007	0.693 ± 0.006	0.809 ± 0.005	0.903 ± 0.003	0.999 ± 0.003
		(0.447 — 0.509)	(0.656 — 0.708)	(0.778 — 0.830)	(0.889 — 0.925)	(0.981 — 1.019)
L. variolus	11	0.489 ± 0.004	0.699 ± 0.006	0.853 ± 0.004	0.903 ± 0.002	0.998 ± 0.004
		(0.476 — 0.511)	(0.678 — 0.711)	(0.833 — 0.864)	(0.887 — 0.913)	(0.980 — 1.022)

Conclusions

The vertical acrylamide gel electrophoretic patterns of the hemolymph proteins provide an excellent taxonomic character for the separation of the two sibling species *L. mactans* and *L. variolus*, at least in one geographic area, and this technique should prove useful in further systematic studies of the genus *Latrodectus*. Its usefulness would be considerably enhanced if we had additional information on geographic variation in this character and knowledge of the functional nature of the various protein fractions from the hemolymph, particularly that of fraction 3. Unfortunately little is known about the biochemistry of spider hemolymph and even less about that of *Latrodectus* species. Boyd (1937) published serological evidence for the presence of hemocyanin in *Latrodectus* and Finlayson (1937) reported the presence of a protein-like, toxic substance he called arachnolysin.

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A NEW GENUS OF THE *TRACHYSPHYRUS* GROUP FROM SOUTHERN BRAZIL (HYMENOPTERA, ICHNEUMONIDAE)*

By Charles C. Porter

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The author has completed a revision of the South American species of the mesostenine genus *Trachysphyrus* Haliday (scheduled to be published during 1967 as a *Memoir* of the American Entomological Institute). In the course of this study there were discovered a few small groups of species definitely related to *Trachysphyrus* but apparently distinct enough to warrant recognition as separate genera. Some of these genera have already been described (Porter 1963, 1965). Several more, limited to the Chilean faunal region, are currently in manuscript and will be published as a unit at a later date. The present contribution treats an isolated and aberrant form known only from the southern Brazilian states of Santa Catarina and Rio Grande do Sul.

Nelophia, new genus

Flagellum: female: definitely flattened below toward apex, 1st segment 6.1-6.5 as long as deep apically; male: segments of about proximal 3/4 with dense, erect setae beneath only for a short distance near base and apex, of distal 1/4 with progressively more extensive erect setae below; 1st segment 4.0 as long as deep apically. *Front:* unarmed, only weakly excavated. *Ocellar Area:* only slightly raised. *Clypeus:* rather low, blunt, asymmetrically subpyramidal in profile, gently and a little convexly sloping upward to near apex and then more steeply and a little concavely declivous; apical margin slightly convex. *Mandible:* 2.5-2.7 as long as wide across base of teeth; teeth subequal. *Occipital* and *Hypostomal Carinae:* occipital carina moderately low above, becoming a rather high flange laterally, lower again close to juncture or near-juncture with hypostomal carina; hypostomal carina very high, about 1/4-1/3 as high as basal width of mandible, rather concave and scoop-shaped. *Pronotum:* dorsal margin a little swollen, with a shallow and obscure submarginal groove; epomia a long, sharp, oblique carina in scrobe, much weaker and prolonged only a short distance below, not defining a discrete swelling or lappet-like area above; anterior margin rounded-off or

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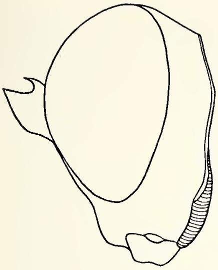

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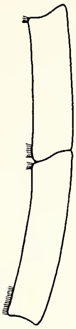

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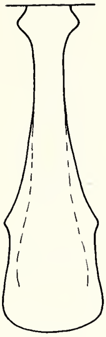

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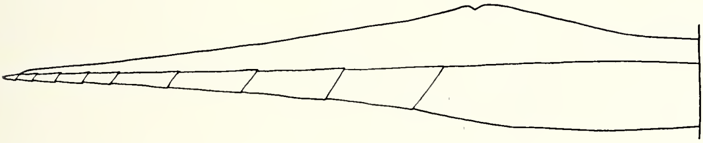

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Figure 1. *Nelophia compsa.* Side view of female head.
Figure 2. *Nelophia compsa.* First two flagellar segments of male.
Figure 3. *Nelophia compsa.* Dorsal view of female first gastric segment.
Figure 4. *Nelophia compsa.* Side view of ovipositor tip.

weakly angled toward mid-height laterally. *Notauli:* rather shallow and narrow, traceable 1/2 or a little more the length of mesocutum. *Mesopleuron:* subalarum a little swollen, not especially expanded; only a very tiny carina on prepectus near hind-corner of pronotum. *Wing-Venation:* radial cell 4.1-4.2 as long as wide, about 1/3 its length removed from tip of wing; areolet moderately large, rather high, intercubiti strongly converging above, 2nd abscissa of radius 0.4-0.6 as long as 1st intercubitus; 2nd recurrent approximately vertical, almost straight or slightly curved on upper 1/2; disco-cubitus gently curved to weakly angled, a short to moderately long ramellus near middle; nervulus interstitial to antefurcal; mediella slightly arched in female, a little more definitely arched in male; upper part of nervellus in female 1.6-2.0 as long as lower, in male 1.1; axillus close to hind-margin of wing. *Propodeum:* spiracle 2.0-2.5 as long as wide; slightly elongate in profile (a little more elongate in male), basal face gently arched and weakly sloping behind, apical face as long as basal and quite steeply declivous; basal trans-carina mostly fine and sharp but somewhat irregular medially and laterally, more generally weak and irregular but traceable in male; apical trans-carina wanting, except for the rather large and conspicuous subligulate to ligulate cristae; median and lateral longitudinal carinae vague or absent; pleural carina weak and irregular. *1st gastric segment:* in both sexes with a large, bluntly triangular lateral expansion at base of petiole; petiole long and slender; postpetiole only weakly expanded, 0.9-1.0 as wide apically as long from spiracle to apex in female, 0.8 in male; petiole without distinct longitudinal carinae or with only a trace of dorso-lateral and dorsal carinae, especially near apex; postpetiole with ventro-lateral longitudinal carina strong, dorso-lateral carina weakly suggested, and dorsal carinae vague or absent. *2nd gastric tergite:* in both sexes with mostly superficial punctation and largely well-separated setae. *Gaster:* unusually long and slender fusiform, somewhat compressed toward apex. *Ovipositor:* sheathed portion 0.3-0.4 as long as fore-wing; straight, moderately slender, strongly compressed; nodus distinct, with a small, sharp notch; dorsal valve with a long, almost direct taper between notch and apex; ventral valve on tip with fine, well-spaced, oblique ridges; tip 0.19-0.22 as high at notch as long from notch to apex.

Type Species: *Nelophia compsa,* new species.

Discussion: *Nelophia* belongs to the subtribe Mesostenina of the geline tribe Mesostenini, as defined by Townes and Townes (1962, pp. 7, 32-33). Here its weakly arched mediella, elongate propodeal spiracle, and large, dorsally narrowed areolet all suggest a close relationship to *Trachysphyrus.* From *Trachysphyrus Nelophia* differs most strikingly because of its more slender habitus (in female), apically flattened female antenna, discontinuous erect setae of male flagellomeres, very high and scoop-shaped hypostomal carina, large expansion at base of petiole, essential absence of longitudinal carinae on petiole, and slender female postpetiole. This is a combination of characters unapproached by any known South American species of *Trachysphyrus,* although some of these features are found singly in a few widely separated species representing diverse phyletic lines within that genus.

The closest relatives of *Nelophia* are probably in the complex subandean and pampal north-central Argentine radiation of the genus *Trachysphyrus,* particularly among certain as yet undescribed forms of the *Albitarsis* Species Group. This genus may thus be interpreted as an aberrant subtropical offshoot of a basically temperate assemblage.

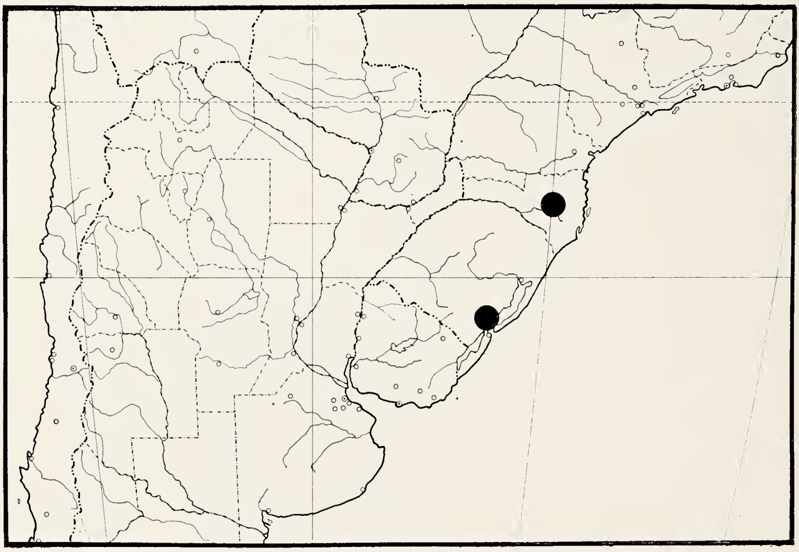
Generic name: *Nelophia* is derived from the Greek *ne-*, a negative prefix, and *lophia*, a "crest" or "ridge".

1. **Nelophia compsa,** new species

Figures 1-4. Map 1.

Types: *Holotype:* (female) BRAZIL (*Santa Catarina:* Nova Teutonia, October 1964, Fritz Plaumann) (Museum of Comparative Zoology, Cambridge, Mass.). *Paratypes:* (2 females and 1 male) BRAZIL (*Santa Catarina:* Nova Teutonia, 300-500 m., January 8, 1953, Fritz Plaumann; *Rio Grande do Sul:* Pelotas, October 9, 1956, C. Biezanko) (Canadian National Collection, Ottawa, Canada; Michigan State University, East Lansing, Mich.).

Female: *Color:* antenna black, more or less brownish-stained below toward apex, a ventrally more or less incomplete white annulus on flagellomeres 5 (apex) to 11 or 12 (in part); head, mesosoma, and gaster black, rather dully pale reddish more or less as follows: often on many cephalic and thoracic sutures; toward lower hind-corner of mesopleuron; more broadly on lower or apical 1/2 of metapleuron; often slightly on propodeum margining apical white bars; on 1st gastric segment broadly below and laterally and somewhat above near base and often subapically; and sometimes a little subapically and on thyridial region of 2nd gastric tergite; the following white: about basal 1/2 of mandible; very large blotch on clypeus; most of face; orbits — narrowly interrupted opposite anterior tentorial pit, broadened below in front to fuse with white on face, and broadened below behind to include almost all of malar space; broad anterior margin of pronotum except near apex; broad dorsal margin of pronotum except on median 1/3 and sometimes near apex; tegula; subalarum; short bar on mesoscutum just above and in part a little behind tegula; about anterior 2/3-3/4 of scutellum; more or less of postscutellum; very large blotch on mesopleuron; hind-margin of mesopleuron; most of metanotum laterally; large blotch on apical 1/2 of metapleuron; small (sometimes vague) to large blotch in laterobasal area and elongate blotch on hind-face of propodeum, from crista (inclusive) to apex; broad apical band and sometimes more or less fragmented lateral stripe on 1st gastric segment; broad lateral and somewhat narrower apical (subapical or sometimes wanting on 2nd tergite) bands on tergites 2-4; and narrower apical bands, becoming much broader laterally, on succeeding tergites; fore-coxa pale red, broadly white-blotched anteriorly, more or less darkened exteriorly above behind white blotch; fore-trochanter and femur pale yellowish red-brown, fore-tibia and tarsus more yellowish; mid-coxa and trochanter pale red, coxa with a moderately large white blotch above anterolaterally; mid-femur blackish with red-brown staining, especially basad, apicad, and within; mid-tibia and tarsus yellowish; hind-coxa, trochanter, and narrow base of femur pale reddish, femur mostly black, tibia and tarsus yellow; wings hyaline, with a small whitish area at base of stigma. *Length of fore-wing:* 8.3-9.2 mm. *Malar Space:* 0.7-0.8 as long as basal width of mandible. *Temple:* 0.4 as long as eye in dorsal view; strongly and almost directly receding; smooth and shining laterally with sharp, medium-sized punctures separated in general by little more to not much less than their diameters, punctures becoming larger, denser, and stronger behind and, especially, above where they are reticulately confluent. *Fore-tibia:* moderately stout, scarcely inflated. *Mesoscutum:* shining with some micro-reticulation and with large, strong, adjacent to reticulately confluent punctures and quite strong trans-biased wrinkles along notauli (mostly within) and with more irregular wrinkling over a large area behind terminus of notauli. *Mesopleuron:* speculum swollen, shining, often largely invaded by strong punctures and wrinkles;



Map 1. Localities for *Nelophia compsa.*

surface otherwise moderately strongly reticulately wrinkled. *Propodeum:* rather strongly reticulately wrinkled, except more weakly sculptured basad of basal trans-carina. *1st gastric segment:* postpetiole finely to rather strongly and granularly micro-reticulate but becoming smooth and polished apicad, with scattered, small, shallow punctures emitting moderately long, not much overlapping setae mostly apically and laterally. *2nd gastric tergite:* mat to dully shining, finely and granularly micro-reticulate with scattered small to medium-sized, mostly superficial punctures emitting long, rather irregularly spaced setae that average a little to very much shorter than their interspaces. *Gaster:* setae of following tergites more or less consistently overlapping, much denser than on 2nd. MALE: *Color:* differs from female as follows: flagellum less definitely brownish-stained, with a more or less incomplete white annulus on segments 11 (in part) or 12 to 18 or 19 (basally); reddish staining a little duller and less extensive; white blotch on clypeus larger and mostly fused with white on face; white band of dorsal margin of pronotum reaching from opposite end of notaulus only about 2/3 the distance to tegula; white on mesopleuron broken up into a large blotch on lower 1/2 anteriorly and a smaller, detached blotch in hind-corner; apical margin of mesopleuron more dully whitish; no white laterally on 1st gastric segment; lateral and apical white bands on tergites 2-4 narrower, subapical band on 2nd especially narrow and brownish-suffused; fore-coxa black with piceous staining and broadly white anteriorly; fore-trochanter whitish below; white blotch on mid-coxa much smaller; hind-legs broken off beyond coxa. *Length of forewing:* 8.4 mm. *Malar Space:* 0.7 as long as basal width of mandible. *Temple:* 0.5 as long as eye in dorsal view. *Gaster:* slender, compressed toward apex, setae about as in female.

SPECIFIC NAME: *Compsa* is derived from the Greek adjective *kompsos*, which means "elegant" or "pretty".

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THE STRUCTURE AND RELATIONSHIPS OF *STEFANOMIOPTERA* GUTHÖRL (MIOMOPTERA-PALAEOMANTEIDAE)[1]

By F. M. Carpenter

Harvard University

During the past 80 years the Upper Carboniferous strata of the Saar Basin in Germany have yielded many interesting and important insects. Most of these have been described by Dr. Paul Guthörl of Bildstock (Saar) over a period of nearly thirty years, from 1934 until his death in 1963. Among the last of the fossils which he described were two species belonging to the order Miomoptera — an extinct group which seems to have been related to the Protorthoptera and possibly to the Psocoptera. The order is known mainly from Permian deposits (Kukalová, 1963) but three species described by Guthörl have been found in the Upper Carboniferous beds of the Saar Basin.[2] One of these, *Archaemioptera carbonaria* Guthörl, which was placed in a separate family (Archaemiopteridae), is distinguished by the oval shape of the hind wing and minor venational features. The other two species, *Stefanomioptera hangardi* (type-species of the genus) and *S. ostertali,* were described as having certain venational structures (such as the origin of the media from the radial sector) which are not characteristic of the order and which would actually eliminate the insects from that taxon. Further study of the fossils seemed to me to be necessary, especially in view of their geological age. Both specimens were originally part of Dr. Guthörl's personal collection but were eventually located by Dr. Dora Wolansky in the Geologisches Institut der Universität des Saarlandes. I am grateful to Dr. Wolansky and to Professor Dr. F. Firtion of the Institut for making possible my study of these two interesting fossils.

For reason given below I am now convinced that the peculiarities which Guthörl attributed to the insects are not actually present in the specimens, that the species are typical Miomoptera and that the genus is a synonym of *Palaeomantis.* New descriptions and figures of these fossils are included here.

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[1] This research is aided by Grant No. GB 2038 from the National Science Foundation.

[2] Another species, *Metropator pusillus* Handlirsch, from the lower part of Pennsylvanian period (Upper Carboniferous) apparently belongs to this order. See Carpenter, 1965, p. 175.

Family Palaeomanteidae Handlirsch

Genus *Palaeomantis* Handlirsch

Palaeomantis Handlirsch, 1904, Mem. Acad. Sci. Petersb., **16**: 4.
[Synonyms: *Delopterum* Sellards, 1909; *Pseudomantis* Martynov, 1928; *Leptoneurula* Martynov; *Pseudodelopterum* Martynov; *Delopsocus* Tillyard; *Miomantisca* Zalessky, 1956; *Delopteriella* Zalessky, 1956; *Miomatoneurites* Zalessky, 1956; *Stefanomioptera* Guthörl, 1962 (new synonymy).]

This genus has now been found in Permian deposits in the United States, Czechoslovakia, and the Soviet Union. The two following species are the only Upper Carboniferous ones known in the genus or family.

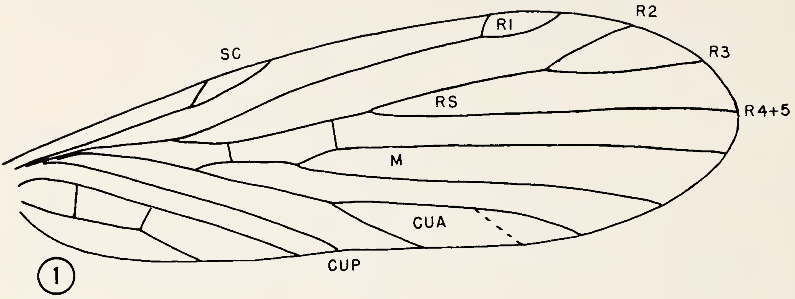
Palaeomantis hangardi (Guthörl)

Stefanomioptera hangardi Guthörl, 1962, Palaeont. Zeitschrift, Schmidt Festband: 69, fig. 3; plate 6, figs. 1a-d.

Fore wing: length, 6.3 mm., width, 2.0 mm. Sc terminating before the middle of the wing and bearing a distinct fork distally; R1 with an oblique distal veinlet; Rs with three terminal branches, R2, R3, R4+5; M arising as usual from CuA at about the level of the origin of Rs, with a deep fork, both branches apparently simple; anterior branch of CuA with a distal veinlet directed to the hind margin; CuP straight. The wing is uniformly covered with fine hairs.

Holotype: No. 1 in the Guthörl Collection, Geol. Inst. Univ. Saarlandes. Collected in Upper Carboniferous beds (Stephanian A), near Neunkirchen, Germany. This is a complete and well preserved fore wing.

In his drawing of this specimen, Guthörl showed M arising from Rs and he designated that as the basis of the genus *Stefanomioptera.* However, the origin of M from CuA, as in all other known Miomoptera, can be distinctly seen in the type specimen, especially when the surface of the specimen has been moistened with water or alcohol. Guthörl's drawing also missed completely all of CuP; this is usually a weak vein in the Miomoptera and can easily be overlooked; application of alcohol to the specimen brings this vein out clearly. With these corrections made, *S. hangardi* is a typical *Palaeomantis,* differing from other species in the minor details of branching and wing shape.



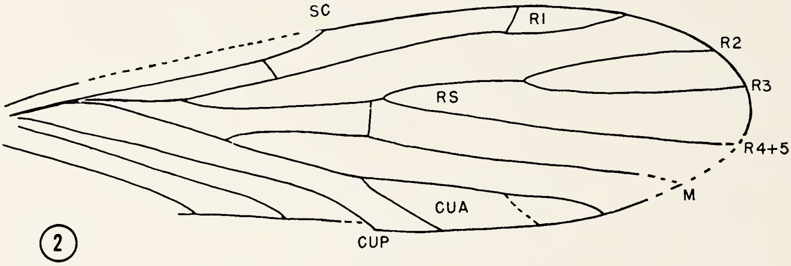


Figure 1. *Palaeomantis hangardi* (Guthörl), from Saar Basin (Upper Carboniferous), Germany; original drawing, based on the type specimen. Length of wing 6.3 mm.

Figure 2. *Palaeomantis ostertali* (Guthörl), from the Saar Basin, Germany; original drawing based on the type specimen. Length of wing, 7.2 mm.

Palaeomantis ostertali (Guthörl)

Stefanomioptera ostertali Guthörl, 1962, Palaeont. Zeitschrift, Schmidt Festband: 69, fig. 4; plate 7, figs. 1a-c.

Fore wing: length, 7.2 mm., width 2.0 mm. The wing is slightly distorted along the posterior margin, just basal of the end of CuP and the anterior margin is missing near the base. Sc, R1 and Rs are formed much as in *S. hangardi*; M arises from CuA, as is typical of the Miomoptera but appears to be without a branch or fork. CuP is straight, as in *hangardi.* This wing is also covered with fine hairs.

Holotype: No. 2 in the Guthörl Collection, Geol. Inst. Univ. Saarlandes. Collected in Upper Carboniferous strata near Neunkirchen, Germany. This is a nearly complete wing, slightly torn along the posterior margin.

Guthörl's drawing shows a small distal fork on M; however, the membrane in that region is broken away and does not, in my opinion, show a fork. In any event, M is unbranched at least until near the wing margin. M does not arise from Rs, as described by Guthörl, but is derived from CuA, as in other Miomoptera. This can be seen by wetting the surface of the fossil. I do not, however, see the distal fork which Guthörl shows on R4+5; it is also in the part of the wing which is broken away.

This species may be the same as *hangardi,* but since it has been described and named by Guthörl, retention of it as a distinct species seems advisable until more is known about the variation within these Carboniferous Miomoptera.

The occurrence of these palaeomanteids, of small size and with reduced wing venation, in Upper Carboniferous strata is unexpected and truly remarkable. On the basis of their wings, they seem to be very much like the Permian forms. Indeed, so far as the wings are concerned, the Miomoptera as a whole form a very homogenous group. The body structures, which are known only in *Palaeomantis,* appear generalized and are not especially suggestive of close relationship to any living order; however, the presence of distinct, though small, cerci (Carpenter, 1939) is indicative of orthopteroid affinities.

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EFFECTS OF ARMY ANT QUEENS ON LONGEVITY OF THEIR WORKERS (FORMICIDAE: DORYLINAE)[1]

By Julian F. Watkins II[2] and Carl W. Rettenmeyer[3]

Many species of ants can be kept readily for months or years in laboratory nests in which survival and colony growth are probably greater than that in the ants' natural environment. If worker ants are kept without their queen(s), survival of adult ants sometimes does not appear to be greatly decreased. For example, we have kept *Camponotus pennsylvanicus* (DeGeer), *Pogonomyrmex occidentalis* (Cresson), and *P. barbatus* (F. Smith) in laboratory nests without queens for 10 to 20 months. Although some of the workers often lay eggs, the colony gradually dies out. Skaife (1961: 141) determined the longevity of *Iridomyrmex humilis* Mayr by keeping about 3,500 workers in a nest without brood or queen. Half the workers died in ten months, and all were dead in 15 months. However, if the results of our experiments are applicable to other ants, isolating ants from their queens will greatly reduce survival.

There is evidence that queen ants influence the development or survival of a brood, but we have been unable to find data regarding the survival of adult workers. Brian and Hibble (1963) reported that *Myrmica* queen heads crushed in ethanol suppressed, and mandibular glands in paraffin oil stimulated, the growth of brood. Brian (1957) and Brian and Carr (1960) found that queens of *Myrmica scabrinodis* and *M. rubra* increased early larval growth, caused a smaller pupal size, improved survival of the brood, and diminished the production of gynes. Carr (1962) reported that dead queens of *Myrmica* also produced a measurable effect on the growth of larvae.

Army ants are among the most difficult ants to keep alive in lab-

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oratory nests. Colony samples with a queen and brood often can be kept for several months, but most of the brood is eaten; usually no further eggs are laid. We have seen no sign of eggs laid by workers in nests without queens. We had one queen of *Neivamyrmex nigrescens* become physogastric in the laboratory and lay eggs. Some of these developed into adult workers, but the size of the brood was much smaller than broods found in the field. Since workers with queens seemed to live longer than those without queens, we did the following experiment.

LONGEVITY OF WORKERS HOUSED WITH AND WITHOUT QUEENS

One thousand workers from the same colony of *Neivamyrmex carolinensis* (Emery) were placed in each of eight laboratory nests. One queen from the same colony having multiple functional queens was also placed in each of four of these nests. Ants in each nest were fed daily the same number of live German cockroaches *(Blatella germanica)* and ant larvae (*Crematogaster* sp.). No brood appeared in any nest. The numbers of live workers were counted after 30 days (Table 1). The queens remained alive and active throughout the test. The mean survival with a queen was 78% higher than the survival without a queen.

Table 1. Effects of queens on the longevity of workers of *N. carolinensis.*

Replica	No. live workers after 30 days		Probability
	Queen and workers	Workers only	
1	466	27	< 0.005
2	629	462	< 0.005
3	627	296	< 0.005
4	623	531	< 0.010
Means	586	329	< 0.005

In a similar experiment, 2,000 workers of *Neivamyrmex carolinensis* were placed in each of four laboratory nests, and three queens from the same colony were put in each of two nests. At the end of 30 days, all workers in nests without queens were dead, but more than 50% of the workers and two of the three queens in the other nests were alive.

ATTRACTION OF WORKERS HOUSED WITH AND WITHOUT QUEENS TO QUEEN SECRETIONS

After army ant queens have stood on a paper surface, workers from their colony will be attracted to the paper (Schneirla, 1953; Watkins and Cole, 1966). Watkins and Cole showed that workers were more attracted to secretions of pheromones deposited by their own queens than to those of conspecific queens from other colonies. They also reported that workers of *Neivamyrmex nigrescens* (Cresson), *N. opacithorax* (Emery), and *N. pilosus* (F. Smith) that had been kept in laboratory nests without queens for at least 25 days were more attracted to queen secretions than were workers housed with queens.

The comparative attraction of workers of *N. carolinensis* housed in laboratory nests with and without queens was tested using methods similar to those described by Watkins and Cole (1966), except all 15 untreated squares of a 16-square grid were used as controls rather than a single untreated square. More than four times as many workers, housed without a queen for 16 days, were attracted to the queen-square compared with the number of workers attracted when kept with a queen (Table 2).

Table 2. Attraction of workers of *N. carolinensis* from the laboratory nests with and without queens to conspecific queen secretions.

Trials	Days	Total ants on squares		Prob.
	without ♀	♀-sq.	u-sqs.	♀ : u
1	16	81	36	< 0.001
2	0	45	10	< 0.001
3	16	124	33	< 0.001
4	0	1	11	> 0.70
5	16	105	81	< 0.001

Means: workers without queen attracted to queen square, 103.
workers with queen attracted to queen square, 23.
Probability of means: < 0.001.

♀-sq. = 1 square on which queen had been placed.
u-sqs. = 15 untreated squares.

LICKING OF QUEENS BY WORKER ANTS

Army ant queens probably are licked more frequently than queens of other species of ants. The extent of such licking under conditions approximating a natural bivouac is difficult to observe directly because the queens often are covered by dense masses of workers. Schneirla (1944) reported that worker army ants licked the intersegmental membranes, hypogynium, and vaginal regions of physogastric queens. Rettenmeyer (1963: 350-352) showed that workers were much more attracted to the gaster of their queen than to her head or thorax, but there was no consistent preference for any part of the gaster.

Five physogastric queens and approximately 5,000 workers of *N. carolinensis* from the same colony were observed in laboratory nests to determine which areas of the queens' bodies were licked most often. The numbers of workers licking each queen's mouthparts, head, alitrunk, legs, petiole, and gastric segments 1, 2, 3, 4, and 5 were counted every 15 minutes for five hours (Table 3).

Table 3. Areas on live queens of *N. carolinensis* licked by their workers.

No. observations	Mean number of workers licking queens										
						Gastric segments					
	MP	H	A	P	L	1	2	3	4	5	Total
20	0	.25	.55	.05	.15	.20	1.00	.60	.95	1.60	5.35
19	.16	.11	.42	.05	.16	.47	.79	.53	1.11	1.78	5.59
20	0	.10	.45	.10	.25	.25	.60	.55	1.20	2.60	6.10
19	0	.53	.42	0	.11	.11	.47	.47	.84	.95	3.90
20	.20	.50	.70	.10	.15	.25	1.10	1.55	1.70	2.00	8.25
Total	.36	1.49	2.54	.30	.82	1.28	3.96	3.70	5.80	8.93	29.19

MP = mouthparts; H = head; A = alitrunk; P = petiole; L = legs.

In 98 observations of the five queens, workers licked all areas of the queens' bodies but consistently licked the fifth gastric segment most frequently. Based on means of all observations, the areas licked in decreasing frequency were: fifth, fourth, second, and third gastric segments; alitrunk; head; first gastric segment; legs; mouthparts; and petiole.

Hagan (1954) reported two pairs of glandular cell masses were arranged in the vicinity of the vulva of queens of *Eciton hamatum*. These masses have ductules extending through the exoskeleton. The physogastric condition of the queens or the presence of such glands may be responsible for the licking being concentrated on the last two gastric segments.

SUMMARY AND DISCUSSION

Worker army ants live for a longer time in the presence of their queen(s), most likely because secretions are licked from the body of the queen. The workers must carry and transmit the effect of their queen because each worker cannot lick the queen frequently. As Brian and Carr (1960) reported for *Myrmica*, the effects of the queen do not persist with the workers but the queen's presence is essential. It is unlikely in these experiments that eating of brood increased worker survival. It is also possible that the presence of a queen modifies the amount of worker activity, but no quantitative data on this are available. Workers were not seen to feed the queen, so probably mandibular or other secretions from the head of the queen are not involved in this longevity factor. If mouth-to-mouth trophallaxis occurred only at night, we would not have detected it.

Workers of *Neivamyrmex carolinensis* also became more attracted to chemicals deposited on paper by their queen after the ants had been kept in laboratory nests without queens for 16 days. When a queen is removed from an army ant colony in the field, the workers usually start "backtracking" or running along previous emigration and raid trails of the colony. Since more workers are attracted to the queen substance after they have been deprived of it for a number of days, this would be a mechanism for increasing the number of workers running along the backtracking columns. The ability of the workers to detect where a queen has stood suggests that they may be able to distinguish chemical trails along which a queen has run. Field observations in Panama with *Eciton* colonies from which queens have been removed showed that the workers primarily run along previous emigration trails but run to a lesser extent on raid trails never used by queens. Backtracking and the ability of the workers to detect traces of a queen clearly are adaptations for colony survival. If a queen is lost by falling from an emigration route, these mechanisms increase the chances that the workers will find their queen. Colonies which do not have queens either die or combine with another colony (Rettenmeyer, 1963: 309). A colony is unable to replace a queen that dies, except under the unusual condition where young queens are already developing within it. The ability to detect traces of a queen along trails of other colonies may provide the stimulus for colony fusion.

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THE FEMALE SEX OF THE MUTILLIDAE SUBFAMILY EOTILLINAE (HYMENOPTERA)[1]

By Clarence E. Mickel

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The subfamily Eotillinae was proposed by Schuster (1949) to include two new genera, *Prototilla* from the Argentine Republic and *Eotilla* from Chile, both based only on the male sex. A female of this subfamily was recently sent to me by Dr. Howard E. Evans, Museum of Comparative Zoology, Cambridge, Mass., with the comment that it had been included in a shipment of ants sent by the Instituto Miguel Lillo, Tucumán, Argentine Republic. The data label on the specimen listed only "Covunco" as the locality, without indication of province or country. Covunco is situated in the province of Neuquén, Argentine Republic, at 70.15 W and 38.31 S.

Four possibilities present themselves for the identification of this specimen, there being no biological or other evidence to correlate this female with any described male: (1) it may be the female of *Eotilla mickeli* Schuster, which was recorded from a number of localities in Chile in the original description; it agrees with this male in having unarmed tarsal claws, but it differs in lacking a distinct petiole, in having the pedicel of the antennae longer than the first flagellar segment and in the distribution pattern of the waxy-white plumose scales on the thorax and abdomen; (2) it may represent an undescribed species of the genus *Eotilla*; without any information as to the specific characters of *Eotilla* females and in particular of *Eotilla mickeli* Schuster, there is no basis for making a decision on this alternative; (3) it may be the female sex of *Prototilla anomala* Schuster described from "Argentina", but without any other information as to locality; it differs from the male *Prototilla anomala* in having the claws unarmed, in having the abdomen entirely black, and in lacking any white subplumose vestiture; (4) it may represent an undescribed species of the genus *Prototilla*; here again, without any information as to the specific characters of *Prototilla* females, there is no basis for making a decision; in fact, the only circumstance that would justify placing this specimen in the genus *Prototilla* is that both come from the Argentine Republic, while *Eotilla* is only recorded from

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[1] Paper No. 6317 Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, Minnesota 55101.

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Chile. It may be that the genus *Eotilla* is limited to Chile and that the genus *Prototilla* is limited to the Argentine Republic, but there is no factual evidence to support this view and the evidence from the geographical distribution of other Chilean and Argentine insects suggests that either genus could have a wider distribution than the country of the type locality.

Alternative (1) appears to be preferable to the others because it seems the most likely, considering available evidence, and if it should prove incorrect the nomenclatorial changes necessary would not be of major import.

Eotilla mickeli Schuster.

Eotilla mickeli Schuster, Ent. Amer. (n.s.), **29**: 77-80, Pl. xii, figs. 1-5, Pl. xiii, figs. 6-11, Pl. xiv, fig. 17, Pl. xv, figs. 18 and 19, ♂. 1949

Female. Black, except antennae, mandibles, trochanters, anterior third of front, and pronotum, stramineous to castaneous; vestiture consisting of black subplumose setae and waxy-white plumose scales as described and figured by Schuster for the males; antennae 12-segmented; labial palpi 4-segmented, maxillary palpi 6-segmented; eyes ovate, strongly facetted; thorax tripartite, superficially bipartite, the mesonotum very narrow, inconspicuous, transverse, but visible; felt lines of second tergum present, but narrow and inconspicuous, approximately half the length of the tergum. Length, 4.5 mm.

Head wider than the thorax, one and one-third the width of the pronotum anteriorly; mandibles falcate, simple, slender, edentate at the tip and with a small tooth within near the tip; proximal half of mandibles stramineous, the distal half castaneous; clypeus small, convex, its anterior margin entire, straight, clothed with black setae and waxy-white scales; antennal tubercles simple; scape terete, slightly arcuate, without carinae beneath, slightly longer than the pedicel, the latter slightly longer than the first flagellar segment; scape and pedicel testaceous, the flagellum somewhat infuscated and darker; front and vertex, except the posterior margin of the latter, clothed throughout with sparse black setae, and waxy-white scales, the latter close and largely obscuring the sculpture of the integument, which appears to be finely granulose.

Pronotum narrowed from front to rear, the anterior margin one and one-half times the width of the posterior margin, weakly, finely granulose, clothed with sparse black setae and with separated waxy-white scales at the anterior margin, and a few scattered ones along the lateral margins; mesonotum narrow, transverse, inconspicuous; propodeum wider than the mesonotum, thus the thorax appearing constricted at the middle; dorsum, posterior face and sides of propodeum weakly, finely granulose, with sparse black setae, and the dorsum with a U-shaped mark of waxy-white scales, the sides of the U at the lateral margins and the base at the posterior margin, thus the anterior and lateral margins of the pronotum and the lateral and posterior margins of the dorsum of propodeum outlined by an irregular line of waxy-white scales, the lateral marginal lines only very slightly discontinuous on account of the very narrow, transverse mesonotum; pleural areas weakly, finely granulose, clothed with scattered waxy-white scales, but the latter more numerous on the meso-metapleural area; legs clothed with sparse black setae and with scattered waxy-white scales on the coxae, trochanters, femora and tibiae; tarsal claws simple, not toothed; pulvillus absent; calcaria 1-1-2, white.

Abdomen without a distinct petiole, the first segment greatly narrowed anteriorly, triangular in outline, nodose, but approaching subsessile to the second segment; first tergum finely, weakly punctate, clothed with sparse black setae and with a pair of spots at the postero-lateral margins of close, waxy-white scales, the two spots separated by a distance equal to one-third the width of the posterior margin of the tergum; second tergum shining, with fine, weak, separated punctures, clothed with sparse, black setae, and with a pair of spots at the postero-lateral margins of close, waxy-white scales, the two spotes separated by a distance equal to half the width of the posterior margin of the tergum; felt lines of second tergum composed of fuscous hairs, inconspicuous; remaining terga shining, with weak, fine, separated punctures and clothed only with sparse, black setae; pygidial area undefined.

Female, Covunco, (Argentine Republic), January 18, 1949. In Instituto Miguel Lillo, Tucumán, Argentine Republic.

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A REVIEW OF THE TAXONOMY AND MORPHOLOGY OF THE BEROTHIDAE, WITH THE DESCRIPTION OF A NEW SUBFAMILY FROM CHILE (NEUROPTERA)

By Ellis G. MacLeod[1] and Phillip A. Adams[2]

Introduction

Collections of Neuroptera which we have received from Chile contain a series of specimens of an unusual berothid representing an undescribed subfamily. Study of these specimens has convinced us that, in addition to throwing new light on the probable evolutionary relationships within the Berothidae, the new form makes somewhat easier an understanding of some of the structural peculiarities of the more-specialized species of this family.

The description of the new subfamily has thus been combined with a reexamination of certain aspects of the morphology of berothids and a redefinition and generic synopsis of the subfamilies. These points will be considered in detail following the taxonomic description of the new form.

Cyrenoberotha, new genus

Figures 9, 14-17

Description. Head capsule and mouthparts, particularly palpi, elongate (figs. 1, 2, 3, 4); vertex moderately elevated, without raised tubercles; head not particularly inflated behind eyes; antenna moniliform, with short scape. Prothorax (fig. 1) somewhat more elongate and less robust than usual in this family. Prosternum small, quadrangular. Legs slender, setose, without raptorial modifications. Abdomen short, ninth tergite distinct from ectoproct in both sexes; callus cerci of ectoprocts present, with trichobothrial setae.

Male (figs. 7, 8, 9): 10th sternite not discernible beneath anus. Gonarcus arms disconnected medially, with 9th gonocoxites (= "parameres")[3] articulated to ventral tips of arms, these latter

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[3] The reasons for the adoption of the terminology utilized here for the internal male genitalia have been briefly outlined by Adams (1967). A short discussion of the modified terminology which we have applied to the female terminalia of berothids is given on p. 247 of the present paper.

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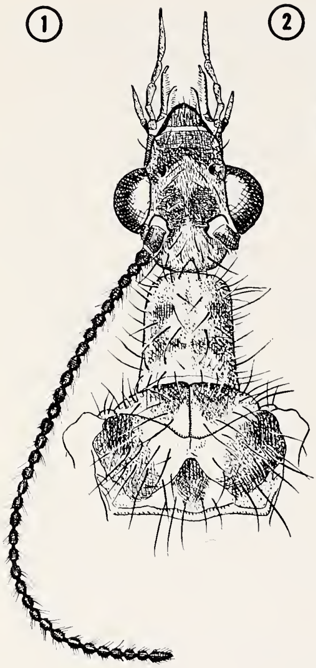

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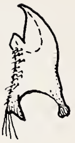

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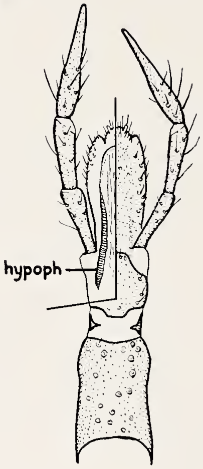

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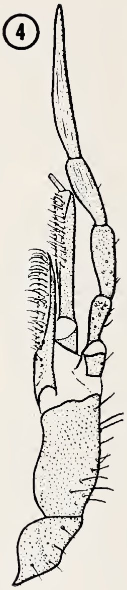

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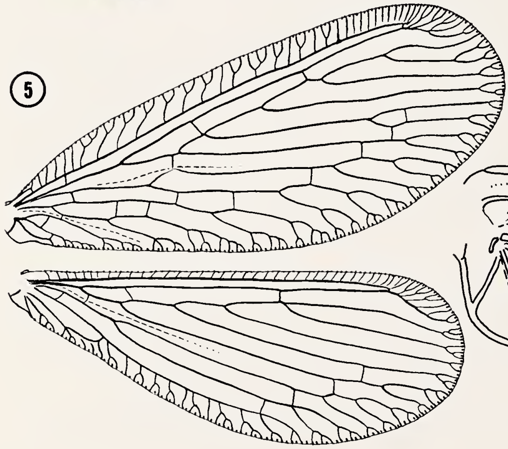

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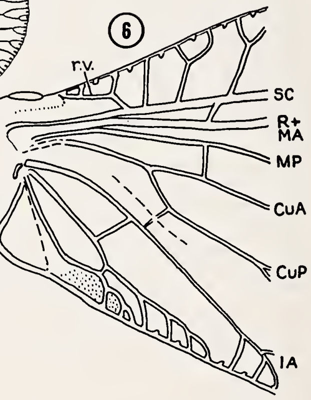

MACLEOD AND ADAMS — BEROTHIDAE

expanded distally with prominent apical teeth; mediuncus (= "pseudopenis", "penisfilum") detached from gonarcus, base laterally compressed forming an elongate sclerite and median apodeme in dorsal wall of ductus ejaculatorius, free distal portion rodlike, lacking setae at tip.

Female (figs. 14, 15, 16, 17): 7th sternite slightly desclerotized at posterior midline; 8th sternite (= "subgenital plate") divided into large, bilateral fragments which are somewhat posteriorly displaced beneath 9th tergite; 8th gonocoxities (= "postgenitale") reflexed dorsally toward genital chamber (figs. 14, 15, 16, 8 gcx); 9th gonocoxites (= "gonapophyses laterales") fused to 10th sternite apically; 9th gonapophyses represented by micro-imbricate lobes which when pressed against 8th gonocoxites close genital chamber ventrally (figs. 14, 15, 9 gph); bursa copulatrix widely open to genital chamber medially, with bilateral pouches opening to medial portion through narrow slits (fig. 14, cop. b.); spermatheca opening broadly from median roof of bursa (fig. 14, sp; fig. 17), continuing as a simple but intricately coiled tube and connecting via a short duct (fertilization canal) to common oviduct (figs. 14, 17, fert. c.); collaterial gland unbranched (fig. 14, coll. gl.); gonopore opening through anterior surface of genital chamber, just behind posterior margin of 8th gonocoxites (fig. 15, gpr.).

Wing tips (fig. 5) bluntly rounded. Forewing: small recurrent humeral vein present (fig. 6, r.v.). Sc distally either connected to R by a crossvein, or these veins sometimes fused at a point. R few-branched, with two radial crossveins; M separate from R to base, diverging at level of humeral vein. MP and Cu dichotomously branched (except at margin). One series (the outer) of gradate veins. Hindwing: recurrent humeral vein absent, discal area almost devoid of crossveins, except for a few outer gradates. Basal piece of MA (= "r-m crossvein") straight, vertical. CuA parallels wing

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EXPLANATION OF PLATE 31

Figs. 1-4 based on paratypes, Figs. 5-6 on ♂ holotype. *Cyrenoberotha penai* n. sp.: Fig. 1. Habitus of head, pro- and mesothorax, head rotated anteriad. Fig. 2. Mandible, anterior aspect. Fig. 3. Labium — posterior surface on right, insert on left showing anterior surface and hypopharynx. Fig. 4. Anterior surface of right maxilla. Fig. 5. Right wings. Fig. 6. Detail of base of right forewing.

Abbreviations: 1A — first anal vein; CuA, CuP — anterior and posterior branches of cubital vein; hypoph — hypopharynx; MP — posterior branch of median vein; R + MA — fused base of radial and anterior median veins; r.v. — recurrent humeral vein; Sc — subcostal vein.

margin for a long distance, with 12-15 pectinate branches; no trace of CuP visible; cu-1a crossvein moderately long, sinuous.

This genus differs from all known berothids in the absence of any trace of fusion of the 9th tergite and ectoprocts, the possession of a recurrent humeral vein in only the forewing, and in the ventrally extended head capsule and correlated attenuate mouthparts.

We take pleasure in naming the type species after its collector, the prominent Chilean naturalist, Luis E. Peña.

Cyrenoberotha penai new species

Head: anterior tentorial pits prominent; labrum about 2/3 as long as broad, rest of head brown; face and vertex with white setae, those on vertex curved forward. Antennae: fossae widely separated, located high on face; scape short, pedicel as long as 2 flagellar segments, flagellum dark; flagellar segments 35 in male, 31-34 in female, shorter in female than in male; setae white, not in definite whorls.

Pronotum longer than wide (mean total length, ♂ — 0.48, ♀ — 0.60; midline length, ♂ — 0.40, ♀ — 0.43; width, ♂ — 0.40, ♀ — 0.48 mm); not especially robust, brown with paler anterior median stripe; with erect white setae (fig. 1).

Prescuta pale posteriorly; scuta pale in middle third; scutella pale along anterolateral margins (fig. 1). Anterior cervical sclerite straight, stiff, slender; 1.8 times as long as posterior cervical in male; 2.5 times as long in female. Pleurae brown.

Legs slender, tibiae pale at middle; tarsi pale basally. Leg setae mostly pale, inclined at about 45°, length at most about twice leg diameter. No tibial spurs. The 4 basal tarsomeres each with a pair of stout setae, on apicolateral corners of plantar surface. Claws slender, strongly curved, without teeth; arolium small.

Wings: membrane transparent, without markings; veins uniformly brown-fuscous. Forewing — costal area slightly broadened at base; middle costal veinlets with 2 or 3 branches; apical veinlets not forked; R dips posteriorly at apex; Rs 4-5 branched; MA forks near margin; 4-5 outer gradates. A thyridium at intersection of ma-mp crossvein with MP1. Hindwing — costal area narrow; 2-4 outer gradates.

Setae on dorsal surface of forewing erect, dark; near wing base, about twice as long as average distance between veins; shorter apically; on ventral surface and both surfaces of hindwing, setae shorter, directed basally at about 75° to long axis of vein. Posterior margin of both wings basally fringed with long, straight, white setae.

Abdomen: brown, unmarked; setae mostly pale, those on membranous areas with prominent dark bases. Male (figs. 7, 8, 9): apex enlarged. Ninth sternite produced, apex bluntly pointed, with tuft of vertical white setae; a prominent marginal tooth each side. Ninth tergite extends farther ventrad than lateral margins of 8th sternite, forming articulation with 9th sternite. Ectoprocts produced, clasper-like; callus cerci pale. Lobes between the gonarcus arms with oval, well-separated scales; between gonocoxites and a median area ventral to mediuncus with larger, imbricate scales; gonocoxites with prominent tooth on expanded apical portion; free portion of mediuncus (fig. 8, mu) bent dorsally, recurved distally. Female (figs. 14, 15, 16): ectoprocts short; eighth gonocoxites little sclerotized, anterior margin deflexed, incised medially. Accessory gland reservoir bulbous, duct connecting reservoir to genital chamber lined with microtrichia. Spermathecal duct from bursa copulatrix dilated, large, more weakly sclerotized than remainder of spermatheca. Spermathecal coiling pattern as in fig. 17.

Measurements (mm, range, means in parenthesis), n = 8♂, = 10♀: forewing length, ♂ — 6.7 (7.06) 7.6, ♀ — 6.5 (7.08) 8.0; body length, ♂ — 4.7 (5.2) 5.5, ♀ — 4.3 (5.1) 5.7; antenna length, ♂ — 3.5 (3.7) 4.1, ♀ — 2.7 (3.0) 3.1; tenth flagellar segment (two of each sex measured), ♂ — length 0.11, width 0.06, ♀ — length 0.08, width 0.06.

Leg segments of a ♂ with a 7.6 mm forewing: coxae .74/.55/.48; femora 1.02/.98/1.15; tibiae 1.0/1.17/1.92; tarsi .83 (.28 — .16 — .12 — .09 — .16)/.65/.78.

Sexual dimorphism, common in some berothids, is limited to the larger eyes, proportionately narrower face, longer antennae with more, elongate segments, and shorter cervical sclerites in the male. No squamae or other setal modifications are present in either sex.

Holotype, a pinned ♂: Coquimbana, North of Huasco River, Atacama, Chile; x-20-1957; L. E. Peña, collector (Museum of Comparative Zoology, Harvard University — type #31568). Paratypes (all coll. by L. E. Peña) — Atacama, Coquimbana, N. of Huasco R.; x-20-57: 1♀. Quebrada Algodon, near Carrizal Bajo; x-18-1957: 8♂, 56♀. x-20-1957: 1♀. Coquimbo, Tofo; x-27-1957: 2♀. (U. S. National Museum, British Museum (N. H.), Adams Coll., MacLeod Coll., Tjeder Coll.).

The gut contents of two specimens consist of pollen grains of *Salix* (identified by D. L. Walkington).

Discussion. Perhaps the sclerites which we have identified in the female as separated fragments of the 8th sternite could be equally as well regarded as derivatives of the 9th tergite, but since an 8th

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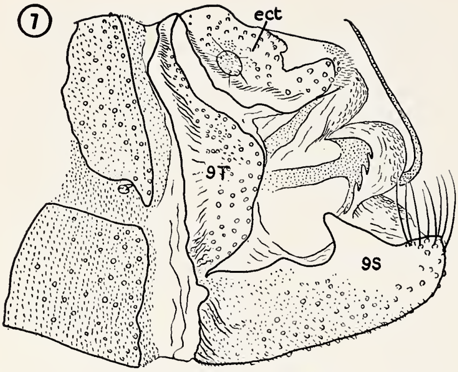

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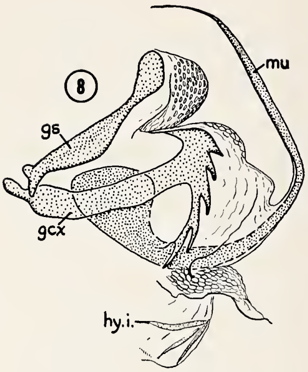

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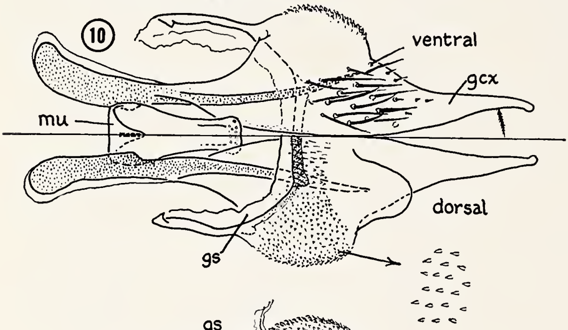

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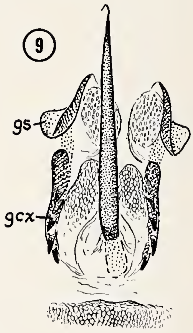

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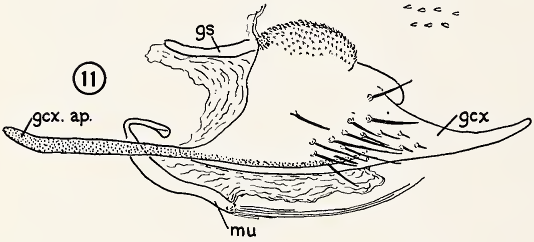

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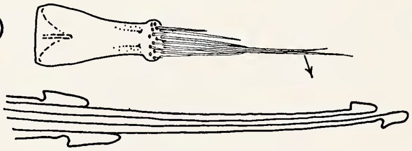

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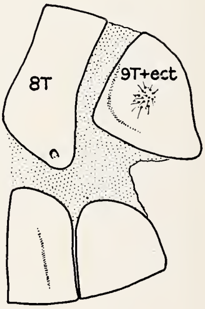

MACLEOD AND ADAMS — BEROTHIDAE

sternite, in some cases very large (cf *Nosybus*), is present in nearly all berothids and is usually bilobed it seems unlikely that such an alternative interpretation is correct.

The only other Berothidae described from southern South America are *Naizema patagonica* Navás and *Espetera mendozina* (Esben-Petersen). Neither of these has been adequately known and because of the presence of recurrent humeral veins in the wings of *N. patagonica*, doubt has been expressed that this species is even a berothid (Carpenter, 1940; Tjeder, 1959). While it has not been possible to examine Navás' type of *N. patagonica,* male and female cotypes of *E. mendozina* have been loaned to us for study. Examination of these specimens and of Navás' descriptions of *N. patagonica* (1919, 1929) has convinced us that Esben-Petersen's species is certainly congeneric with *N. patagonica* and, indeed, is very likely the same species. Although it shows no close similarity to *Cyrenoberotha,* a redescription and catalogue of *Naizema* will be presented here as the rather unusual structures of this group provide insight into some of the structural specializations of the Berothinae.

Naizema Navás

Figures 20-25

Naizema Navás, 1919, Rev. R. Acad. Cienc. Madrid 17: 298-299.

Type species (by original designation): *Naizema patagonica* Navás. Navás, 1929, Mem. Acad. Cienc. Zaragoza 2: 19-20. Handschin, 1935, Rev. Suisse Zool. 42: 700. Carpenter, 1940, Proc. Amer. Acad. Arts

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EXPLANATION OF PLATE 32

Cyrenoberotha penai n. sp.: Figs. 7-9 of ♂ holotype. *Lomamyia squamosa* Carpenter, ♂: Figs. 10-13, drawn from a specimen from 3 mi. NW of La Palmilla on Highway Sur No. 19, B. Calif., Mexico; 18-1-59; H. B. Leech Col.; in the collection of the California Academy of Sciences. This specimen is the same as that studied and figured by Acker (1960), where it is identified as "*Lomamyia* sp."

Fig. 7. Lateral aspect of terminalia. Fig. 8. Detail of gonarcus, gonocoxites, mediuncus and hypandrium internum, drawn after the removal of these structures from the abdomen, lateral aspect. Fig. 9. Same as Fig. 8, posterior aspect. Fig. 10. Divided dorsal and ventral views of fused gonarcus and gonocoxites and of mediuncus (terminal tuft of setae of mediuncus omitted), inset showing detail of microtrichia on surface of gonarcus. Fig. 11. Same, lateral view. Fig. 12. Ventral view of mediuncus, inset showing detail of tips of two longest (median) pairs of setae. Fig. 13. Lateral view of terminal abdominal segments of abdomen.

Abbreviations: ect — ectoproct; gcx — gonocoxite; gcx. ap. — basal apodeme of gonocoxite; gs — gonarcus; hy. i. — hypandrium internum; mu — mediuncus; 9S — 9th sternite; 8T, 9T — 8th, 9th tergites; 9T+ect — fused 9th tergite and ectoproct.

Sci. 74: 256. Tjeder, 1959, South African Animal Life 6: 260.
Espetera Navás, 1929, Mem. Acad. Cienc. Zaragoza 2: 29.
Type species (by original designation): *Berotha mendozina* Esben-Petersen. Tjeder, 1959, South African Animal Life 6: 293. NEW SYNONYMY.

Description. Face short, hardly extending ventrad of eyes; anterior vertex tubercle transverse, confluent with well-demarked lateral tubercles; vertex and area behind eyes inflated. Scape length equals about 4/5 eye diameter; flagellum stout, segments short, wide. Mouthparts sunken into ventral concavity of head, mandibles nearly vestigial, maxillae and labium greatly reduced. Pronotum transverse, arched, lightly sclerotized, two transverse furrows. Trichobothrial setae present at apex of abdomen but callus cerci poorly delimited.

Male (figs. 20, 21, 22): ninth tergite and ectoprocts fused, ninth sternite a narrow band, tenth sternite absent. Gonarcus desclerotized medially, articulated laterally to apodemes of ninth tergite. Gonocoxites articulated to gonarcus arms laterally; space between gonarcus and gonocoxites weakly desclerotized dorsally. Rectangular median sclerite extending from gonarcus to mediuncus pouch. Mediuncus withdrawn and coiled in deep pouch, bearing lateral arms and long terminal setae.

Female (figs. 23, 24): 7th sternite large, desclerotized posteromedially and weakened along ventral midline. Eighth sternite bandlike. Ninth tergite discernible but fused with ectoprocts. Ninth gonocoxites with hypocaudae represented by short tubercles. Ninth gonapophyses developed as short projections from posteromedial surfaces of ninth gonocoxites, inserted into transverse, cup-like eighth gonocoxites to close genital chamber. Copulatory bursa large, membranous, widely confluent with genital chamber. Spermathecal duct short, membranous. Spermatheca with a thin-walled, saccate, expansible posterior diverticulum and a short, tubular anterior extension which is convoluted and weakly sclerotized.

Forewing (fig. 25): elongate, apical and posterior edges straight (♀) or concave (♂). Recurrent humeral vein present; Sc apically connected to R by a crossvein; base of M distinct from R, fusing for a distance beginning at level of recurrent humeral vein. Inner gradate series well-developed; outer series sometimes absent. Hindwing: Sc connected to R by a crossvein; recurrent humeral vein present; MA branches from the stem of M and fuses with R basad of level of recurrent vein (difficult to see, because of the proximity of M and R, basally); stem of MP not fused with R basally. Vestige of distal portion of CuP extending basad from cu-a crossvein. Single gradate series; 3-4 crossveins. No squamae on wings or body.

Discussion. This genus is quite similar to *Trichoberotha* Handschin in the structure of the head capsule and prothorax, in the presence of recurrent humeral veins in both pairs of wings, in the general plan of venation, and in the small band-like shape of the eighth sternite of the female. *Trichoberotha* has larger mandibles, no trace of fusion of the bases of M and R in the forewing, and shows several important differences in the structure of the male and female genitalia.

Naizema mendozina (Esben-Petersen), n. comb.

Berotha mendozina Esben-Petersen, 1912, Entomol. Mitteilungen 1:271, fig. 5 (male terminalia). Described from three cotypes now in the Universitetets Zoologiske Museum, Copenhagen. We designate as lectotype a pinned male of this series bearing the following labels: "Mendoza 1904-05 A.C.J.H."; "Coll. Esben-Petersen"; "Type"; and "Berotha mendozina n. sp., Type!". The cleared abdomen is in glycerine in a glass microvial on the pin with the specimen.

Espetera mendozina Navás, 1929, Mem. Acad. Cienc. Zaragoza 2: 30-31, figs. 10 (male terminalia), 11 (photograph of wings).

Distribution. Argentina: Mendoza-Santa Rosa, Potrerillos.

Naizema patagonica Navás

Naizema patagonica Navás, 1919, Rev. R. Acad. Cienc. Madrid 17: 299-300, fig. 5 (drawing of wing bases). Type, stated to be in Navás Coll., not examined. Navás, 1929, Mem. Acad. Cienc. Zaragoza 2: 20-22, fig. 7 (drawing of wing bases), fig. 8 (drawing of forewing).

Distribution. Argentina: Patagonia.

NOTES ON THE MORPHOLOGY OF THE TERMINAL ABDOMINAL SEGMENTS OF BEROTHIDAE

Several inconsistencies and errors have entered the literature on berothid genital morphology since most previous studies have dealt with rather specialized forms. In the male, Carpenter (1940) interpreted the reduced sclerite of the fused gonarcus and gonocoxites of *Lomamyia* as representing the apparently missing "10th tergites" (ectoprocts), while Tjeder (1959) did not realize that both gonarcus and gonocoxites (parameres in his terminology) are represented in the seemingly single sclerite of *Acroberotha xiphophora* Tjeder. The generalized arrangement of these sclerites shown by *Cyrenoberotha* (as well as by *Nosybus* and *Naizema*) indicates that in the specialized, higher berothids the gonocoxites have become much reduced with the weakly sclerotized space between them and the gonarcus becom-

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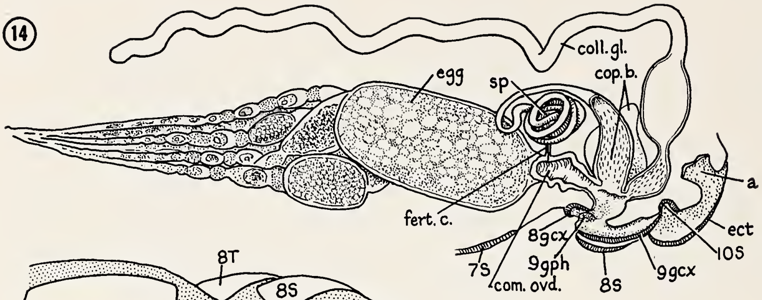

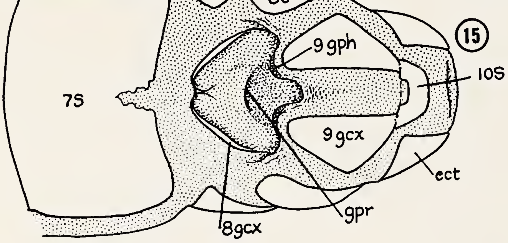

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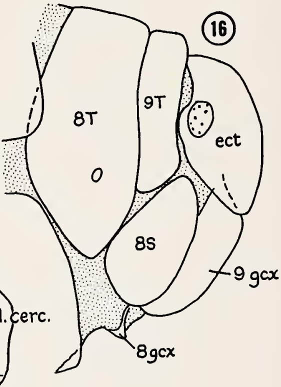

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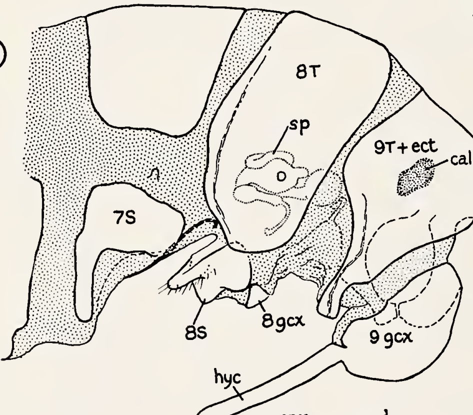

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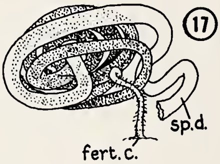

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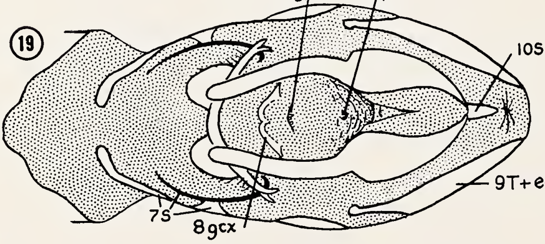

MACLEOD AND ADAMS — BEROTHIDAE

ing so narrowed that a condition has been reached where there seems to be only a single sclerite (figs. 10, 11, gs. gcx). The presence of setae on this structure provides confirmatory evidence of its composite origin since in our experience the gonarcus rarely bears setae while the gonocoxites usually do.

The free, distal portion of the mediuncus frequently undergoes extreme elongation in different groups of berothids, producing an attenuate structure which may be further increased in length by the presence of long setae at its distal end. This elongate organ is carried, in the manner of a coiled watch spring, in a reflected internal pocket of membranous cuticle. The male of *Naizema mendozina* which we have illustrated (figs. 21, 22) illustrates a moderate development in this direction. Tjeder (1954) has applied the term "penisfilum" to such specialized mediunci. At the opposite extreme, species of *Lomamyia* have the distal portion of the mediuncus reduced so that only the basal sclerite in the dorsal wall of the ejaculatory duct remains (figs. 10, 11, 12, mu). In this genus a distal tuft of fine, short setae with specialized tips is present without any elongation of the mediuncus (fig. 12).

The system of homologies we have used for the external female genitalia is based upon an extensive study of neuropteran genitalia, which will be published elsewhere. A large 8th sternite, bearing setae, is readily identifiable in most Sialodea and many Planipennia.

Explanation of Plate 33

Cyrenoberotha penai n. sp.: Figs. 14-17, based on several ♀ paratypes. *Lomamyia flavicornis* (Walker), ♀: Figs. 18-19, drawn from a specimen from Washington, D. C., Rock Creek Park; 10 June 1958 (M58-25#10); E. MacLeod Col.; in MacLeod collection.

Fig. 14. Detail of internal genital anatomy, lateral view, showing connections of median oviduct, spermatheca, bursa copulatrix and colleterial gland. External cuticle depicted as in median longitudinal section. Fig. 15. Ventral view of terminal abdominal segments. Genital chamber, depicted as seen when 8th gonocoxites are drawn anteriorly away from 9th gonapophyses. Fig. 16. Terminal abdominal segments, lateral view. Fig. 17. Spermatheca. Fig. 18. Terminal abdominal segments, lateral view, genital chamber depicted as opened slightly by posteriad retraction of ventral process of fused 9th tergite + ectoproct from its usual articulation against posterior end of 8th sternite. Fig. 19. Same, ventral view.

Abbreviations: a — anus; cal. cerc. — callus cercus; coll. gl. — colleterial gland; com. ovd. — common oviduct; cop. b. — bursa copulatrix; ect — ectoproct; egg — mature oocyte in lateral oviduct; fert. c. — fertilization canal; 8gcx, 9gcx — 8th, 9th gonocoxites; 9gph — 9th gonapophysis; gpr — gonopore: exit of median oviduct into genital chamber; 7S, 8S, 10S — 7th, 8th, 10th sternites; sp — spermatheca; sp. d. — spermathecal duct; 8T, 9T — 8th, 9th tergum; 9T+ect — fused 9th tergite and ectoproct.

Posterior to the 8th sternite, but anterior to the genital opening, a shiny, seta-less sclerite is often found which may bear two processes posteriorly (e.g., in Sialodea, Psychopsidae, Polystoechotidae). We interpret this sclerite as the fused 8th gonocoxites and the posterior processes as their gonapophyses. We have not seen 8th gonapophyses in Berothidae. A diagrammatically archaic 9th gonapophysis occurs on the medial margin of the ninth gonocoxites in the snake-fly *Agulla*. In Sialodea and Planipennia, the ninth gonapophyses, if present, are represented by small, leaf-like sclerites near the anteroventral corners of the ninth gonocoxites. These appear to have been reported previously only by Principi (1949) and Adams (1967), in the Chrysopidae.

There have been few previous attempts to relate the terminal structures of the female abdomen of the Berothidae to the basic insectan plan of the external sclerites of the female copulatory structures. Carpenter (1940), unaware of the fusion of the ectoprocts with the 9th tergite, mistook the 9th gonocoxites as the "10th tergites". Tjeder (1954, 1959) employed a useful and consistent terminology for the structures we have termed 8th sternite, 8th gonocoxites and 9th gonocoxites, but though his equivalent terms "subgenital plate", "postgenitale" and "gonopophyses laterales" are precise enough for descriptive purposes, they do not relate these sclerites to homologous structures of other insects. His choice of the term "postgenitale" for the 8th gonocoxites is particularly inappropriate since this sclerite is morphologically anterior to most of the female "genital" structures, including the all-important landmark of the gonopore (figs. 15, 19, 8 gcx, gpr).

Except for the morphologically oriented works of Stitz (1909, 1931), Brückner (1935) and Principi (1949, 1954, 1956), none of whom have dealt with berothids, little attempt has been made to depict or interpret accurately the relational morphology of the genital chamber, bursa copulatrix and spermatheca. Taxonomists in particular have failed to appreciate that a large cuticular bursa copulatrix, opening from the genital chamber, is a consistent feature of all Planipennia, with the spermathecal duct serving as a reliable morphological landmark for its location. In addition, they have overlooked the relations of a second duct, connecting the spermatheca to the common oviduct (figs. 14, 17, fert. c.). In the species of *Lomamyia* which we have studied this duct almost certainly conveys the spermatozoa to their point of fertilization in the oviduct. In species of many families (such as many Chrysopidae) the bursa is only narrowly confluent with the genital chamber and is located quite close to the spermatheca to which it is connected by a slit-like opening in its floor. In these groups no appreciable spermathecal duct really exists (cf Principi, 1949: fig. XIV; 1954: fig. V). In the Berothidae (and closely similar Mantispidae) the greatly enlarged bursa is widely confluent with the genital chamber, while the spermatheca, located at a considerable distance from the bursa, is connected to it through a rather long spermathecal duct which is often tortuously looped. Tjeder (1954, 1959) has observed and figured this duct, but has not noted its connection with the bursa except in two cases (1959) where he has misleadingly termed it a "copulatory aperture" (fig. 323) and a "gonopore" (figs. 252, 253). Small spermathecal (accessory) glands have sometimes been recognized (cf Tjeder, 1959, fig. 242), but in several cases the structure which has borne this designation seems to be the fertilization canal connecting spermatheca and oviduct (cf Tjeder, 1959, fig. 313).

Judging from our own work with *Lomamyia* and the published accounts of several other genera (Tjeder, 1959), we believe that a very large spermatophore is probably characteristic of most berothids and that this circumstance probably provides the functional explanation of the wide-mouthed and voluminous structure of their bursae. In our laboratory studies, the formation and fate of these spermatophores was followed on many occasions. Mated females of *Lomamyia* were often observed to carry awkwardly a very large spermatophore protruding from the bursa for several days. During this time eggs, quite predictably, were never laid.

Examination and dissection of spermatophores revealed that invariably they consist of a rather soft, albuminous, outer layer which surrounds a comma-shaped central core of harder material. During the post-copulatory period when a female is carrying her spermatophore, the outer coat is the first portion to wear (or be eaten) away, leaving the exposed central core attached for a somewhat longer time. Inspection of cores from both fresh and worn spermatophores disclosed the unexpected fact that they are traversed throughout their length by a small central canal which is in perfect alignment with the opening of the spermathecal duct in the bursa. Presumably sperm travel up this canal to the spermathecal duct, but just how the precise confluence of the two ducts is achieved during copulation is not yet known. Quite probably the tip of the mediuncus or the tuft of prominent setae from the posterior margin of the mediuncus is inserted into the spermathecal duct during copulation, thus providing an axis about which the inner core of the spermatophore is secreted. However this remains to be verified.

On several occasions females of *Lomamyia* have been collected by us which carried spermatophores in various stages of disintegration, indicating that the fate of these structures in nature closely parallels what we have observed in the laboratory. Tjeder (1954, 1959) also studied field-collected females carrying fragments of spermatophores in two species of *Acroberotha* in which the structure and destruction of the spermatophore seems to be about the same as in *Lomamyia.* He did not, unfortunately, realize that the hard core was an integral part of the spermatophore and concluded that it was a permanent component of the female genital segments in the genus *Acroberotha* to which he applied the term "ovipilum".

When females have removed or lost the last traces of their spermatophores, the very extensive space of the confluent bursa and genital chamber is effectively closed to the outside by the close approximation of various sclerites, with members of different groups of berothids achieving this result by somewhat different mechanisms. The details of these differences have been noted in the descriptions of the subfamilies which we have given below.

THE CLASSIFICATION OF THE BEROTHIDAE

The taxonomy of the Berothidae is still in a rather rudimentary state and the data provided in the present paper can do little more than to suggest what the principal groups and adaptive trends might be. The only world-wide treatments at the species level have been those of Krüger (1922) and Navás (1929). Both of these studies suffer from a heavy reliance on relatively minor details of the wing venation and wing shape, with the resulting generic and suprageneric classification bearing little resemblance to phylogenetic reality. In addition, with the exception of *Nosybus,* all of the species treated in these revisions are relatively specialized forms belonging to the Berothinae, so that little insight into the overall evolution of the family has been gained by their study.

In what is the best account of this family to date, Tjeder (1959) recognized three subfamilies: Rhachiberothinae, containing mantispid-like forms with raptorial forelegs; Berothinae, containing species with elongate, frequently falcate wings and hypocaudae on the 9th gonocoxites; and "Sphaeroberothinae" (i.e. Nosybinae, see below), with short, rounded wings and lacking hypocaudae. In spite of the limitations imposed on him by an inadequate literature and the availability of only a small number of South African species, Tjeder's divisions seem quite sound, although, as noted below, we believe that several of the genera which he referred to the "Sphaeroberothinae" (on the basis of their rounded wing tips) should be reassigned to the Berothinae. In addition it is now necessary to propose a new subfamily for the inclusion of *Cyrenoberotha.*

In the following section we have provided new descriptions for the four subfamilies and have listed all of the described genera. We have had representatives of all of the subfamilies and principal genera available for this study, the specific genera we have examined being marked with an asterisk in the list. Other than the synonymy of *Espetera* and *Naizema* noted above, all described genera are listed without indication of synonymy since so few of the type species have been examined by modern workers. Our views on certain obvious synonymies are set forth in the discussions following the subfamilies.

The four subfamilies of the Berothidae may be distinguished by the following key:

1. Forelegs cursorial; free stem of MA in hind wing vertical, straight 2
   Forelegs raptorial; free stem of MA in hind wing oblique, sinuate .... Rhachiberothinae
2. Ninth abdominal tergite fused with ectoprocts; face very short, not much extended ventrad of lower margin of eyes 3
   Ninth abdominal tergite free from ectoprocts; face conspicuously extended ventrad of lower margin of eyes .... Cyrenoberothinae
3. Bases of R and M fused in forewing, their common stem showing no trace of a composite structure, with MP diverging abruptly from R + MA at an angle exceeding 30°; 8th sternite of female an elongate, triangular sclerite extending posteriorly beneath the fused 9th tergite and ectoprocts and the bases of the similarly produced 9th gonocoxites; hypocaudae lacking .... Nosybinae
   Bases of R and M in forewing usually separate, where closely adajacent or fused these bases usually preserving some trace of their separate origins and with MP diverging from R + MA at a more acute angle which is usually less than 20°; 8th sternite of female not greatly elongate; hypocaudae present (figs. 18, 23) or absent .... Berothinae

Cyrenoberothinae n. subfam.

Description. Berothids with head and mouthparts elongate; vertex lacking tubercles and elongate setae; head capsule not inflated behind eyes. Pronotum elongate, lightly constructed, not markedly deflexed laterally. Forelegs lacking raptorial modifications. 9th abdominal tergite not fused with ectoprocts, the latter with well-developed cercal calluses and trichobothrial setae.

Wings short, with rounded apices; stems of M and R adjacent but separate to base. Forewing with vestige of recurrent humeral vein. Hindwing lacking recurrent humeral vein; with basal free piece of MA vertical and straight; CuP not developed.

Male with 9th abdominal sternite well developed as an elongate subgenital plate, articulating anteriorly on the ventrally extended 9th tergites. Gonarcus membranous in midline; gonocoxites strongly developed and well separated from gonarcus distally, articulating proximally on the latter; mediuncus with a large basal sclerite and apodeme and with a free tubular portion distally, lacking setae at its tip.

Female lacking squamae. 7th abdominal sternite well developed, slightly desclerotized in posterior midline. 8th sternite divided into two bilateral fragments, displaced posterodorsally. 9th gonocoxites lacking hypocaudae, bearing reduced remnants of 9th gonopophyses, these latter affecting closure of genital chamber by anteriad appression against concave surface of 8th gonocoxites. Bursa copulatrix small, widely confluent with genital chamber, with a pair of bilateral pouches. Spermathecal duct short; spermatheca a simple coiled tube, lacking enlargements and diverticula.

Type and sole included genus: **Cyrenoberotha* n. gen. Known only from Chile.

Rhachiberothinae Tjeder, 1959

Rhachiberothinae Tjeder, 1959, South African Animal Life 6: 262.
Type genus (by original designation): *Rhachiberotha* Tjeder, 1959.

Description. Male unknown. Berothids with head and mouthparts short; vertex with at most a slight suggestion of tubercles whose position is marked by a few elongate setae; head capsule moderately inflated behind eyes. Pronotum elongate, lightly constructed, slightly deflexed laterally. Forelegs with raptorial modifications consisting of elongate coxae and swollen femora, with large macrotrichia, against which tibiae and tarsae can be reflexed. 9th abdominal tergite fused to ectoprocts, the latter with reduced or absent cercal calluses and trichobothrial setae.

Wings short, with rounded apices; stems of R and M adjacent but separate to base, or bases of these veins fused in forewing. Recurrent humeral vein not present. Hindwing with basal free piece of MA transverse, sinuate; with base of CuP present, fusing with 1A.

Female lacking squamae. 7th abdominal sternum well developed. 8th sternum reduced to thin cresentic sclerite in midline, or absent. 9th gonocoxites with minute or small hypocaudae; remnants of 9th gonapophyses produced anteriad as slender bands along ventrolateral margins of genital chamber, the gonapophyses affecting the closure of the genital chamber by pressing anteriomesad against convex membranous lobe occupying the usual position of the concave 8th gonocoxites behind region of 8th sternum. Structure of bursa copulatrix unknown. Spermathecal duct elongate; spermatheca complexly coiled, with enlargements and diverticula.

Included genera: **Rhachiberotha* Tjeder, 1959; *Mucroberotha* Tjeder, 1959. Both from Rhodesia.

Discussion. The manner of the closure of the genital chamber described above is based on our examination of specimens of the two species of *Rhachiberotha* and this may not be quite correct for *Mucroberotha.* Judging from Tjeder's figures (1959: figs. 253K-253M), weakly sclerotized 8th gonocoxites ("postgenitale") seem to be present in this latter genus and the closure of the genital chamber may not differ appreciably from the manner described above for *Cyrenoberotha.*

Nosybinae new name

Sphaeroberothinae Krüger, 1922, Stett. Ent. Zeit. **83**: 75. *Nomen nudum.*
Sphaeroberothini Navás, 1927, Bull. Soc. R. Ent. d'Egypte **1926**: 206; 1929, Mem. Acad. Cience. Zaragoza **2**: 68, 106. *Nomen nudum.*
Sphaeroberothinae Tjeder, 1959, South African Animal Life **6**: 281. Type genus (by original designation): *Nosybus* Navás. *Nomen nudum.*

Description. Berothids with head and mouthparts very short; vertex with lateral tubercles well developed and with area of median tubercle raised as a larger, convex swelling which is not distinctly tuberculate, all swellings bearing tufts of long setae; head capsule moderately inflated behind eyes. Pronotum quadrate, lightly constructed, not deflexed laterally. Forelegs without raptorial modifications. 9th abdominal tergite fused to ectoprocts, the latter lacking cercal calluses and trichobothrial setae.

Wings short, with rounded apices; recurrent humeral vein not present. Stems of R and M fused in forewing, closely adjacent but separte to base in hindwing. Hindwing with basal free piece of MA vertical, straight; CuP not developed.

Male with 9th abdominal sternite reduced, transverse. Gonarcus not desclerotized in midline; gonocoxites well developed, widely separated from gonarcus distally, articulating on the latter proximally; mediuncus greatly elongate, withdrawn into an internal pouch.

Female lacking squamae. 7th abdominal sternite well developed. 8th sternite produced posteriad as an elongate triangular sclerite beneath fused 9th tergite + ectoprocts and the bases of the similarly produced 9th gonocoxites, the latter without hypocaudae or traces of 9th gonapophyses. Genital chamber closed by posteriad appression of 8th sternite beneath bases of gonocoxites. Bursa copulatrix small, widely confluent with genital chamber. Spermathecal duct very long; spermatheca a complexly coiled tube, with enlargements and diverticula.

Type and sole included genus: **Nosybus* Navás, 1910. Previously known from southeast and central Africa. We have seen specimens from northern Angola (Malange).

Discussion. The name of this taxon has been a continuing source of confusion, the early proposals of Krüger and Navás being *nomina nuda* since no included genus bore the name *Sphaeroberotha.* Such a genus was not even described until 1930 when Navás proposed this name for his new species *Sphaeroberotha dumonti* and referred to it as "Genus Sphaeroberothinorum" (p. 133) and ". . . de este nuevo género en la tribu de los Esferoberótinos. . . ." (p. 135). We have examined the holotype female of this species and find that this insect is a member of the Berothinae so that if Navás' action of 1930 should be considered as a validation of a family-group name based on *Sphaeroberotha,* this name would fall into the synonymy of Berothinae.

EXPLANATION OF PLATE 34

Naizema mendozina (Esben-Petersen), ♂ (lectotype), ♀ (lectoparatype): drawn from specimens from Mendoza, Argentina; Haarup; in the collection of the Universitetets Zoologiske Museum, Copenhagen.

Fig. 20. Lateral aspect of terminalia of male. Fig. 21. Detail of terminalia of male, posterio-ventral view. Fig. 22. Detail of gonarcus, gonocoxites, mediuncus, and hypandrium internum, lateral aspect. Fig. 23. Terminal abdominal segments of female, lateral view. Fig. 24. Same as Fig. 23, ventral view. Fig. 25. Right forewing of male.

Abbreviations: a — anus; coll. gl. — collaterial gland; cop. b. — copulatory bursa; 8 gcx, 9 gcx — 8th, 9th gonocoxites; 9 gph — 9th gonapophysis; gpr — gonopore; gs — gonarcus; hy. i. — hypandrium internum; mu — mediuncus; 7S, 8S — 7th, 8th sternite; sp — spermetheca; 9T + ect — fused 9th tergite and ectoproct.

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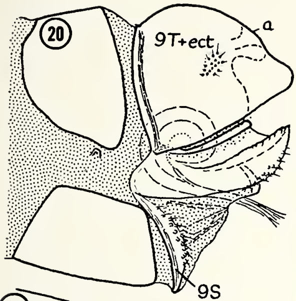

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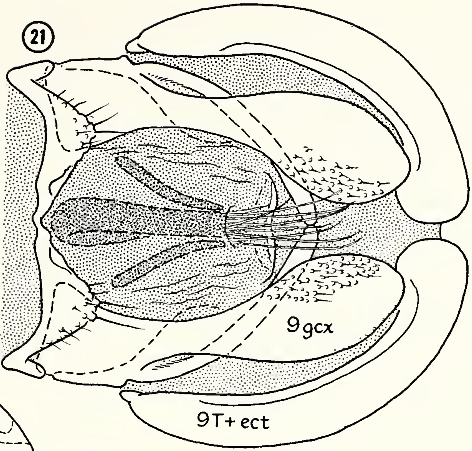

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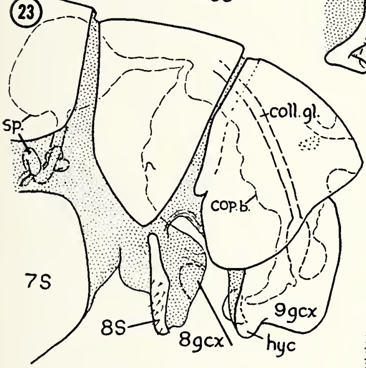

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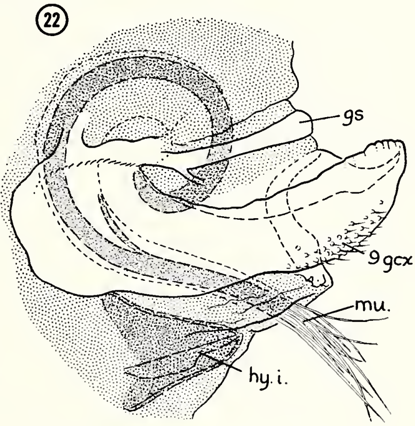

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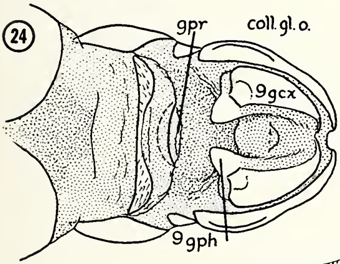

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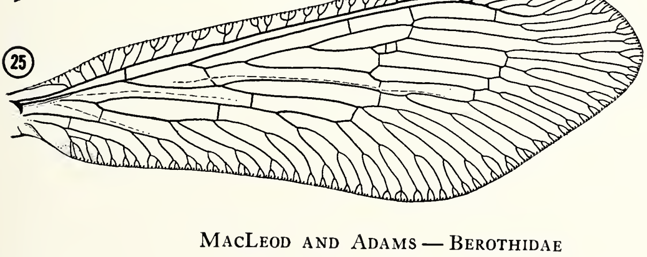

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The final attempt, by Tjeder (1959), to validate the name Sphaeroberothinae (by the designation of *Nosybus* as the type genus) is contrary to the Rules.

It is not possible to resurrect this name for a valid family-group taxon and it is therefore necessary to propose the new name Nosybinae for the taxon to which the name Sphaeroberothinae has previously been applied.

Krüger, Navás, Banks and Tjeder have placed the additional genera *Cycloberotha, Costachillea, Sphaeroberotha,* and *Berothella* in the same suprageneric taxon as *Nosybus.* The only unifying feature of this assemblage has been the short wings with rounded apices. Actually these genera show only a superficial similarity to *Nosybus,* the first three being rather ordinary berothines, with such typical features as well-developed hypocaudae and, in *Cycloberotha* and *Costachillea,* squamae on the wings of the females. The type species of *Berothella, B. phantoma* Banks, has not been available to us for study. The holotype male of the other described species of this genus, *B. pretiosa* Banks, has been examined by us. It is a dilarid, so we have provisionally excluded *Berothella* from the Berothidae pending a study of its type species.[4]

Berothinae Handlirsch, 1908

Berothinae Handlirsch, 1908, Die Fosselen Insekten, p. 42. Type genus (by tautonomy): *Berotha* Walker, 1860. Krüger, 1922, Stett. Ent. Zeit. **88**: 56. Tjeder, 1956, South African Animal Life **6**: 293.

Berothini Banks, 1913, Trans. Amer. Ent. Soc. **39**: 211. Navás, 1921, Ann. Soc. Sci. Bruxelles **40**: 230; 1927, Bull. Soc. R. Ent. d'Egypte **1926**: 206; 1929, Mem. Acad. Cienc. Zaragoza **2**: 23, 105. Handschin, 1935, Rev. Suisse Zool. **42**: 700.

Esferoberótinos, Sphaeroberothinorum Navás, 1930, Broteria **26**: 133-135. Type genus (by tautonomy): *Sphaeroberotha* Navás, 1930. NEW SYNONYMY.

Description. Berothids with head and mouthparts short to very short; vertex with lateral tubercles weakly to strongly developed, anterior tubercle usually not in evidence, vertex with elongate setae which are not necessarily confined to tubercles; head capsule moderately to strongly inflated behind eyes. Pronotum transverse, lightly constructed or elongate and of a more massive construction, always deflexed laterally. Forelegs without raptorial modifications. 9th abdominal tergite fused to ectoprocts, the latter bearing obsolescent cercal calluses and trichobothrial setae.

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[4] The holotype ♂ of *B. phantoma* is now located in the British Museum. At our request, Mr. D. E. Kimmins has examined this specimen and informs us that this species also belongs to the Dilaridae, so that *Berothella* should definitely be removed from the Berothidae.

Wings moderately to strongly elongate with rounded or with subfalcate or falcate apices; recurrent humeral vein present as a vestige or absent; stems of R and M closely adjacent but separate to base or fused for a short distance in forewing. Hindwing with basal free piece of MA vertical, straight; CuP not developed.

Male with 9th abdominal sternite reduced, transverse. Gonarcus arms fused or desclerotized in midline; gonocoxites developed and widely separated distally from gonarcus, or closely adjacent to gonarcus throughout their length; mediuncus represented as a small sclerite or elongate and withdrawn into an internal pouch, always with a tuft of setae at its tip.

Female with squamae on coxae, pleurae, or wings, or else these scales lacking. 7th abdominal sternite well developed, or slightly descelerotized in posterior midline, or showing various degrees of reduction until, at extreme, represented only as small lateral fragments. 8th sternite a small, cresentic sclerite or, more usually, a large frequently complex ventral sclerite. 9th gonocoxites occasionally lacking hypocaudae or with these structures very small, more usually with hypocaudae well developed; traces of 9th gonapophyses lacking. Genital chamber closed by anteriad appression of membranous medial surface of 9th gonocoxites against concave sclerotized surface of 8th gonocoxites. Bursa copulatrix large, widely confluent with genital chamber. Spermathecal duct short and membranous or, more usually, elongate and well sclerotized; spermatheca complexly coiled, with enlargements and usually with diverticula.

Discussion. The following additional family group names have been utilized for various subdivisions of the Berothinae: Trichomatidae Tillyard, 1916 and Trichomatini Navás, 1929; Naizemini Navás, 1921; Spermophorellini Navás, 1921; Nodallini Navás, 1927. These have not been placed in formal synonymy, since some of these may prove valid at the tribal level when the interrelationships of the many genera of the Berothinae have been worked out.

A total of twenty generic names have been used for berothids which belong to this subfamily. These names, with their geographic distribution indicated in parentheses, are: **Acroberotha* Krüger, 1922 (southern Africa, China, Japan, southeast Asia, Australia); **Berotha* Walker, 1860 (Africa, Madagascar, Hindustan, India, Ceylon, Java, Formosa); *Costachillea* Navás, 1929 (north Africa); **Cycloberotha*

Navás, 1929 (Australia); *Dasypteryx* Stein, 1863 (Greece); **Espetera* Navás, 1929 [= *Naizema* Navás, 1919, see above] (Argentina); **Frawalkeria* Navás, 1929 (Borneo, Formosa); *Isocelipteron* Costa, 1863 (southern Europe); *Lekrugeria* Navás, 1929 (India); **Lomamyia* Banks, 1904 (North America, we have also seen a specimen from Zamorano, Honduras); *Naizema* Navás, 1919 (Argentina); **Nodalla* Navás, 1927 (Egypt); *Podallea* Navás, 1936 (Ethiopia); *Protobiella* Tillyard, 1923 (New Zealand); *Sisyrura* Navás, 1905 (China); **Spermophorella* Tillyard, 1916 (Australia); **Sphaeroberotha* Navás, 1930 (Tunisia); **Stenobiella* Tillyard, 1916 (Australia); **Trichoberotha* Handschin, 1935 (Australia); *Trichoma* Tillyard, 1916 (Australia).

Krüger (1923) has also described a species, *Proberotha prisca,* from the Baltic amber; unfortunately this specimen has not been located for study so that its subfamily placement cannot now be ascertained. An undescribed amber berothid in the collection of the Museum of Comparative Zoology which, judging from Krüger's rather incomplete description of *P. prisca,* is probably not congeneric, has long hypocaudae and is obviously a berothine.

The genera *Dasypteryx, Frawalkeria, Isoscelipteron, Podallea,* and *Sisyrura* are obviously very close to *Berotha* and several of these have long been regarded as synonyms of this genus. *Lekrugeria* and *Acroberotha,* although presumed to differ from *Berotha* in the number of branches of the radial sector of the forewing and shape of the apex of the wings, are also at best only poorly distinct and may prove to be synonymous with *Berotha* when the structure of these species becomes known in detail. An appreciation of the variability of such characters as the branching of the radial sector and the shape of the wing apex can be gained from a review of the species of the well-studied genus *Lomamyia.* These show considerable individual variation in the number of branches of Rs, reaching as high as 7 (not counting MA) in some specimens of *L. fulva* Carpenter, and present wing shapes ranging all the way from slightly pointed (*L. longicollis* (Walker)) to species with strongly falcate apices (*L. hamata* (Walker), *L. squamosa* Carpenter). It seems unlikely that stable generic limits will be found utilizing such characters as these.

Notes on the evolution of the Berothidae

The Subfamilies of the Berothidae. An estimate of the overall degree of evolutionary change from the presumed structure of ancestral berothids of eight key genera of the Berothidae is presented in Tables I and II. In this analysis, twenty-three morphological characters, which are judged to be of phylogenetic importance, have been coded into "primitive" and "derived" states by a study of the form of these characters in other groups of present-day Neuroptera. We have regarded as primitive states those which, because of their occurrence in generalized members of related families, are believed to reflect the state of these characters in the common ancestors of these families and, presumably, in the direct ancestors of the Berothidae as well. Derived states are presumed to have departed from the primitive states in the manner specified in Table I. In deducing the states of these characters, particular attention has been paid to their condition in the Mantispidae, Dilaridae, and Neurorthidae[5], since study of both the larval and adult stages of these groups has indicated a close phylogenetic relationship of these taxa with the Berothidae (MacLeod, 1964; MacLeod and Adams, unpublished).

Study of these data emphasizes the evolutionary mosaicism of each of the subfamilies and shows that although there is a preponderance of primitive states in the Cyrenoberothinae, Rhachiberothinae, and Nosybinae, important specializations are present in each of these groups which makes it unlikely that either is ancestral to the other two or to the Berothinae. Thus in the Cyrenoberothinae, the elongate head, non-tuberculate vertex, and divided 8th abdominal sternum of the female are specializations which eliminate this taxon as a candidate for the ancestor of the other subfamilies. Likewise the specialized prothorax and prothoracic legs and the reduction of 8th abdominal sternite in the female rule the Rhachiberothinae out as direct ancestors of the Nosybinae and Berothinae, while the additional specializations of the fusion of 9th abdominal tergite and ectoprocts and the loss of the recurrent humeral vein in the forewing eliminates the Rhachiberothinae from the ancestry of the Cyrenoberothinae as well. Finally the specializations of the fusion of the stems of the radius and media in the forewings and the greatly elongate 9th gonocoxites of the females argue that the Nosybinae could not serve as ancestors of the Rhachiberothinae or Berothinae, while the additional features of the fusion of 9th abdominal tergite and ectoprocts and the loss of the cercal callus removes them as ancestors of the Cyrenoberothinae.

This analysis also emphasizes the rather generalized nature of *Naizema* within the Berothinae and raises the question as to whether

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[5] A study of the adults and presumptive larvae of this group has convinced the senior author that this group should be treated as a distinct family. The evidence justifying this conclusion will be presented in a separate publication.

TABLE I: SUMMARY OF THE DIRECTION OF EVOLUTIONARY CHANGE OF TWENTY-THREE CHARACTERS OF THE BEROTHIDAE

STRUCTURE	CHARACTER STATE	
	PRIMITIVE	DERIVED
1 Face and mouthparts	Short	Elongate
2 Mandibles	Normally developed	Greatly reduced
3 Vertex tubercles	Present, with elongate setae	Absent, vertex setae small
4 Head behind eyes	Not swollen	Swollen
5 Pronotum	Quadrate, lightly constructed, not deflexed laterally	Elongate, heavily constructed, deflexed laterally
6 Prothoracic legs	Cursorial	Raptorial
7 9th tergum and ectoprocts	Separate	Fused
8 Cercal callus	Present, with trichobothrial setae	Absent, lacking trichobothrial setae
9 Wing length	Short	Elongate
10 Wing apex	Rounded	Falcate or truncate
11 Recurrent humeral vein	Present in both wings	Absent in both wings
12 Stems of radius and media	Separate to base in both wings	Fused to base in forewing
13 MA in hindwing	Basal piece oblique, sinuous	Basal piece vertical, straight
14 CuP in hindwing	Present, free of 1A	Not developed
15 Gonocoxites of ♂	Separate from gonarcus distally	Fused throughout length with gonarcus
16 Mediuncus of ♂	Moderately developed, without setae at tip	Reduced, or greatly elongate, with setae
17 Squamae in ♀	Lacking in all species of genus	Present in some species of genus
18 7th sternite of ♀	Normally developed	Reduced to small lateral sclerites
19 8th sternite of ♀	Large, present midventrally	Reduced, or displaced bilaterally, or greatly elongate posteriorly
20 9th gonocoxites of ♀	Small, without hypocaudae	Large, with hypocaudae
21 Bursa	Small	Large
22 Spermathecal duct	Short	Long
23 Spermatheca	Simple coiled tube	With enlargements and diverticula

TABLE II: ESTIMATION OF THE DEGREE OF EVOLUTIONARY CHANGE IN 8 GENERA OF BEROTHIDAE

TAXON	CHARACTER # (FROM TABLE I)																							INDEX OF EVOLUTIONARY CHANGE
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
Cyrenoberotha	2	0	2	0	1	0	0	0	0	0	1	0	2	2	0	0	0	0	2	0	1	0	0	0.28
Rhachiberotha	0	0	1	2	1	2	2	1	0	0	2	0	0	1	*	*	0	0	1	1	—	1	2	0.43
Nosybus	0	0	0	2	0	0	2	2	0	0	2	1	2	2	0	2	0	0	1	1	1	2	2	0.48
Naizema	0	2	1	2	0	0	2	1	2	1	0	1	2	2	0	2	0	0	1	1	2	0	2	0.52
Mucroberotha	0	0	1	2	1	2	2	2	0	0	2	2	0	1	*	*	0	0	2	2	—	2	1	0.55
Stenobiella	0	0	1	1	1	0	2	1	2	2	2	1	2	2	—	—	0	1	0	2	2	2	2	0.62
Cycloberotha	0	0	1	2	2	0	2	1	2	1	2	1	2	2	0	2	2	2	0	2	2	2	2	0.70
Lomamyia	0	0	1	2	2	0	2	1	2	2	2	0	2	2	2	2	2	2	0	2	2	2	2	0.74

The index of evolutionary change for each genus is computed from the numerical total of all character states divided by twice the number of character states used in the computation. Thus an index of 0.0 would result from all characters being in a primitive state, while an index of 1.0 would occur if all characters were in a derived state. Since many of the derived character states involve losses or fusions, this index is also a rough estimate of the degree of specialization of the members of each genus.

0 = primitive character state, 1 = intermediate character state, 2 = derived character state;
* = ♂ unknown, — = information cannot be determined from specimens at hand.

this genus is correctly referred to this subfamily. Our treatment of *Naizema* is based on an examination of the direction of the specializations of this group. Thus the elongation and subfalcation of the wing; elongate, coiled mediuncus with setae at its tip; incipient development of hypocaudae; and the bulb-like enlargement of a portion of the spermatheca are all specializations of a berothine type and argue that *Naizema* has stronger phylogenetic relationships with the other genera of the Berothinae than with any other group. The gap between *Naizema* and other berothines is, however, considerable and tribal distinction may well be justified when more complete knowledge of the other genera of this subfamily is available.

Relationship to the Mantispidae. On the basis of the similarities in the structure of their adults and on certain general parallels in their life histories, Tjeder (1959) pointed out the likelihood of a close phylogenetic relationship between the Berothidae and the platymantispine Mantispidae. Some of the items on Tjeder's list of similarities (1959: 273), such as the pectinate branching pattern of Rs in the forewing, the sinuate course of the base of MA ("r-m vein") in the hindwing, the presence of trichosors, the occurrence of similarly shaped mouthparts, and the similarly shaped distal tarsomere of the anterior leg, actually prove nothing since they occur in many other, distantly related groups of Neuroptera as well. The additional similarity of the fusion of the 9th abdominal tergite with the ectoprocts, noted by Tjeder in *Plega,* seems more likely to be the result of parallel evolution, since these sclerites are unfused in *Cyrenoberotha* and in such generalized platymantispines as *Drepanicus* and *Gerstaeckerella.* We believe, however, that Tjeder's central thesis is certainly corrct and that it is further strengthened by several of the structural details of *Cyrenoberotha* and other generalized berothids.

The form of the gonarcus and gonocoxites of unspecialized berothids such as *Cyrenoberotha, Nosybus, Naizema,* and *Trichoberotha* are very similar to the pattern found in all of the Mantispidae known to us. In these groups the well-developed gonocoxites are widely separated from the gonarcus distally, while these two sclerites form a strong articulation proximally. A strong similarity also exists between *Cyrenoberotha* and many mantispids in the form of the mediuncus which is separated from the gonarcus and has the form of a basal plate in the roof of the ductus ejaculatorius from which a free, posterior extension is developed. Comparisons have previously been drawn (Tjeder, 1959) between the extremely elongate posterior extension ("penisfilum") which the mediuncus undergoes in some genera of both the Berothidae and Mantispidae. Since this modification seems to occur sporadically only among the more specialized members of these families, it seems more likely that this similarity is also the result of parallel specializations from the more generalized type.

Additional close similarities occur between generalized berothids and the Mantispidae in the wide connection between the genital chamber and bursa; in the rather long, narrow spermathecal duct; and in the coiled tubular shape of the spermatheca which lacks prominent dilations. MacLeod (1964) has pointed out additional similarities between these two families on the basis of the structure of the larval head.

The very mantispid-like condition of the forelegs of the Rhachiberothinae suggests that the Mantispidae may have taken their origin directly from members of this group of berothids. However, such features of *Rhachiberotha* and *Mucroberotha* as the fusion of the 9th abdominal tergite and ectoprocts, the presence of hypocaudae, the loss of the recurrent humeral vein, and the development of the very characteristic marginal forking of CuA and the reduction of CuP in the hindwing are all specializations characteristic of the higher Berothidae. Since the great majority of Mantispidae lack these peculiarities, it seems quite likely that these specializations were also lacking in their direct ancestors and that these ancestors must be sought in some other group of berothids or near berothids.

It must be noted, however, that similar specializations occur, with a mosaic distribution, among certain genera of the Platymantispinae. Thus a partial or complete fusion of the 9th abdominal tergite and ectoprocts occurs in *Plega* and *Trichoscelia* (= *Symphrasis*); small tubercles, probably homologous to hypocaudae, are present in *Drepanicus;* and a reduction or loss of CuP in the hindwing is found in *Drepanicus* and *Gerstaeckerella,* while this latter genus shows the loss of the recurrent humeral vein as well. With the exception of the hypocaudae-like tubercles of *Drepanicus,* these are characters involving the fusion or loss of structures and their sporadic occurrence in the Platymantispinae is very likely the result of parallel evolution. The structural heterogeneity of this subfamily does, however, suggest that a similar variability may also have once been present in the Rhachiberothinae, so that the possibility cannot yet be ruled out that the primitive Mantispidae did evolve from some unknown rhachiberothine which lacked the specializations of the more advanced Berothidae noted above.

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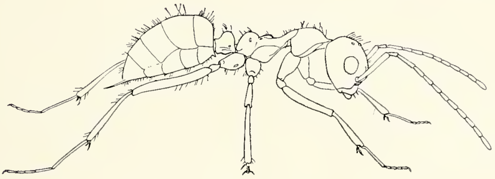

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CRETACEOUS INSECTS FROM LABRADOR
1. GEOLOGIC OCCURRENCE

By Erling Dorf

Princeton University

During the summer of 1958 a collection of fossil leaves and insects was made by the writer from a bed of ferruginous, red argillite associated with so-called rubble ore at the Redmond No. 1 deposit in the Knob Lake district of Labrador. This area is close to the Quebec border about 320 miles north of the town of Sept Iles, which lies along the north shore of the St. Lawrence River. The fossil locality is 10 miles south-southeast of Schefferville, roughly half way between Knob Lake and Astray Lake (in section 260, approximately 600 feet southwest of the 1957 Redmond No. 1 base line).

Fossil leaves were first discovered in this bed by Mr. Donald J. McMahon, geologist of the Development Division, Iron Ore Company of Canada, during the course of trenching operations. A small collection of the leaves was sent to the writer for identifications and age determinations by Mr. Roger Blais, then Development Supervisor of the Iron Ore Company of Canada. Subsequently, Mr. Blais arranged for the writer to visit the locality in September 1958. During this visit the insect remains here described were discovered, in addition to the remains of 36 species of plants, including 1 alga, 4 ferns, 1 lycopod, 3 conifers, and 27 angiosperms (Dorf, 1959).

The field work and subsequent investigation have been jointly sponsored by the Iron Ore Company of Canada and Princeton University.

The 5-foot argillite bed in which the leaves and insects were found lies in the uppermost portion of the Redmond formation, a massive 300 foot unit of rubble ore containing lenses of pale reddish to grayish clay. The argillite bed dips 45 degrees toward the east and has been traced along the strike for about 500 feet below a 10 to 15 foot overburden of glacial deposits. It is believed to be separated from an overlying clay unit by a major fault (Blais, 1959, pp. 282-285, figs. 2, 3).

The argillite is a very distinctive, massive, heavy rock containing about 60 per cent red hematite (Blais, 1959, p. 285). The 5-foot bed is very uniform in composition from top to bottom. It is very finely though inconspicuously laminated, but has a tendency to fracture conchoidally. Fossil plants occur sporadically along occasional poorly developed bedding planes. Even less common are the associated insect remains here described. The depositional setting of the original sediments is believed to have been a shallow lacustrine basin. The flora is interpreted as indicating growth in a humid warm-temperate climate.

An early Late Cretaceous (Cenomanian) age is indicated by the plant remains. Closest correlatives in North America are the Raritan flora of New Jersey, the Dakota flora of the Great Plains, and the Tuscaloosa flora of Alabama. Pollen and spores from underlying clay beds have been interpreted as slightly older Cretaceous (Albian) age (John Grayson, personal communication, 1960).

The rubble ore itself has also yielded plant remains in the form of fragments and a stump of carbonized wood. These occur in the breccias and gravels at the Redmond No. 1 deposit and elsewhere in the Knob Lake district. They have been identified as coniferous wood of Cupressinean affinity and regarded as at least as young as mid-Mesozoic (Usher, 1953, p. 100).

The insects in the argillite bed were sent to Professor F. M. Carpenter for his examination and they were subsequently referred by him in turn to specialists in the four orders of insects represented: Neuroptera, Isoptera, Coleoptera and Blattodea. The neuropteron, a snake-fly, is being described below by Professor Carpenter; the termite, by Professor Alfred Emerson. The beetles, which include several Cupidae, are being studied by Dr. A. G. Ponomarenko (Palaeontological Institute of the Academy of Sciences in Moscow), who has published several papers on Mesozoic Coleoptera. The roaches, which have been given only preliminary study and which present taxonomic problems, will presumably be treated along with the beetles in still another part. Because of the unusual nature of the snake-fly and the termite, descriptions of these are being published at this time without waiting for the completion of the other two parts in this series of papers.

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CRETACEOUS INSECTS FROM LABRADOR
2. A NEW FAMILY OF SNAKE-FLIES (NEUROPTERA: ALLORAPHIDIIDAE)*

By F. M. Carpenter
Harvard University

Among the twelve insects which Professor Dorf collected near Schefferville in Labrador is a neuropteron of the suborder Raphidiodea. This is the first Cretaceous snake-fly to be found, though the group is known from older deposits, Permian as well as Jurassic (Martynova, 1961). The Labrador fossil has more in common with the Jurassic species than with the Tertiary and Recent families, Inoceliidae and Raphidiidae, but clearly represents a distinct family.

Family **Alloraphidiidae,** new family

Related to the Mesoraphidiidae. Fore wing very long and slender; pterostigma well-developed; Sc ending at mid-wing; Rs originating just before mid-wing; MA arising well after the fork of MP and coalesced with Rs for a short distance; CuA connected to M at its point of separation from R. Hind wing about the same size and shape as the fore wing; costal area narrower than that of fore wing; Sc terminating slightly beyond mid-wing; MA arising from R just beyond the origin of MP.

This family differs from the Mesoraphidiidae not only in the extreme wing-length but also in having MA in the fore wing originate well beyond the point of forking of MP, and in having CuA connected to M at its point of separation from R. In the fore wing of the Mesoraphidiidae MA arises from M before or at the origin of MP, and CuA joins M distad of the separation of M from R.

Alloraphidia, new genus

Fore wing about six times as long as wide; costal area widest at about its middle; Sc directed away from the costa slightly in the apical region and giving rise to about six costal veinlets; Rs arising just basad of the end of Sc; Rs and MA each with three well-defined branches, apart from marginal forkings; CuA with a closed submarginal cell. Hind wing: MA very close to MP at their origins; branches of main veins much as in fore wing.

Type-species: *Alloraphidia dorfi,* n.sp.

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*This research has been aided by a grant from the National Science Foundation (GB-2038).

Alloraphidia dorfi, new species

Figure 1.

Fore wing: length 9.5 mm., width 1.6 mm.; pterostigma light yellow (as preserved), short and broad and traversed by a single oblique veinlet; MP with four definite terminal branches; CuA with three branches. Hind wing length 9.0 mm., width 1.8 mm.; pterostigma as in fore wing but slightly narrower; CuA with a distal fork; cross veins shown in text-figure 1.

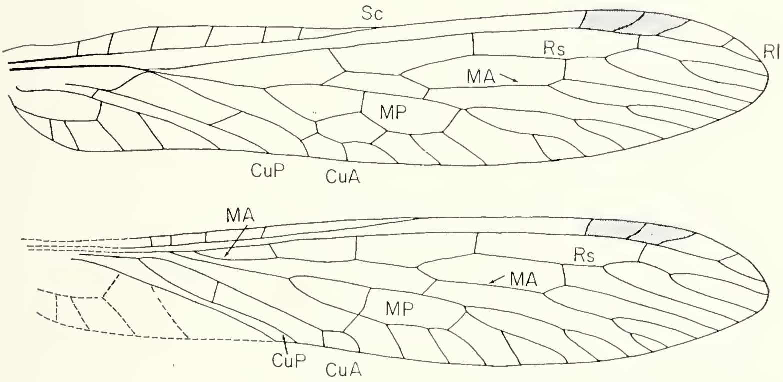
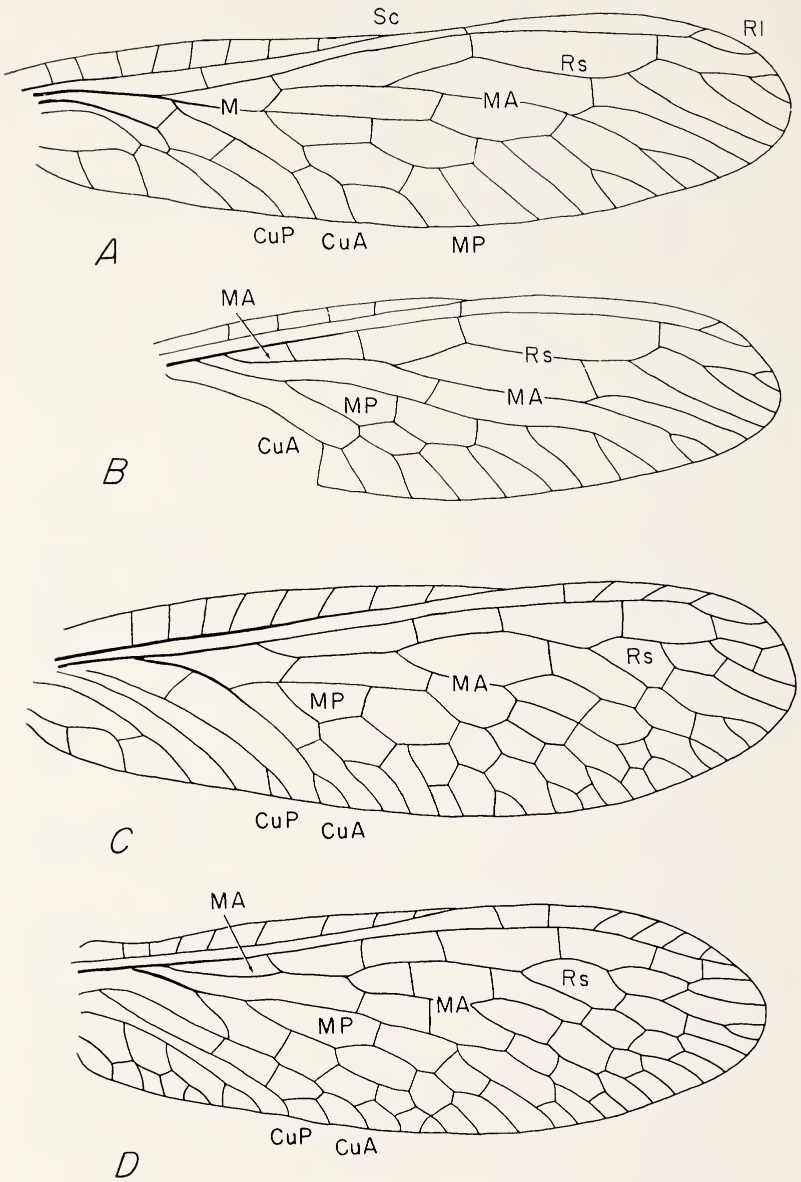


Figure 1. *Alloraphidia dorfi,* n.sp. Drawings of fore and hind wings, based on holotype. Length of wing, 9.5 mm. Cretaceous of Labrador.

Holotype: No. 87269, Invertebrate Paleontology collections, Princeton University. The specimen is preserved in a piece of hard, ferruginous argillite, collected at Redmond No. 1 deposit in Knob Lake District (near Schefferville), Labrador, Canada. Collected by Professor Erling Dorf in 1958. This deposit is apparently late Albian (Early Cretaceous) or Cenomanian (Late Cretaceous) in age, very nearly at mid-Cretaceous.

The specimen consists of a pair of fore and hind wings virtually complete; the wings are almost perfectly superimposed but with just enough discrepancy so that the main veins can be followed separately for each wing, except for the anal area of the hind wing. The preservation is excellent; the pterostigma is light yellow, as in many Recent snake-flies.

On the basis of the wings, *Alloraphidia* seems to be much closer to the Mesoraphidiidae than to the Recent families of the order.



Carrenter — Snake-flies

In the Alloraphidiidae and Mesoraphidiidae MA and MP of the hind wing arise independently from the stem R + M; in the Inocelliidae and Raphidiidae MA and MP arise from the common stem M, after its separation from R. On the other hand, in none of the previously known extinct families, including Mesoraphidiidae, does MA *in the fore wing* arise far distad of the fork of MP, as it does in the Alloraphidiidae. This feature does occur in the Inocelliidae and Raphidiidae, but it is obviously of an independent origin.

The Alloraphidiidae provide additional evidence for the conclusion that in the Mesozoic era the snake-flies were a far more diverse group than now, representing still another line of evolution within the order. In addition to the family Mesoraphidiidae, which is known from the Jurassic of Turkestan, the family Baissopteridae is known from the Upper Jurassic of Trans Baikal; this includes species which had more venational branches and more cross veins than the Mesoraphidiidae or the existing families (Martynova, 1961). It is interesting to note, however, that MA arose in the hind wing of the Baissopteridae just as it does in the Mesoraphidiidae and the Alloraphidiidae (see plate 35). The excellent preservation of the Jurassic snake-flies from the USSR shows clearly that, apart from the wings, their body structure was remarkably like that of the existing families, even to the prothorax and ovipositor (Martynov, 1925b, Martynova, 1962). The Oligocene snake-flies (Baltic amber; Florissant and Creede Shales, Colorado) belong not only to Recent families but to existing genera, though these genera in the Tertiary show quite different distributional patterns from those which they possess now (Carpenter, 1936, 1956).

EXPLANATION OF PLATE 35

Fig. A. *Mesoraphidia pterostigmalis* Martynova, fore wing; Upper Jurassic, USSR (Kazakstan). Length of wing, 13 mm. After Martynova, 1947.

Fig. B. *Mesorophidia pterostigmalis* Martynova, hind wing; Upper Jurassic, USSR (Kazakstan). Length of wing, 12 mm. After Martynova, 1947.

Fig. C *Baissoptera martinsoni* Martynova, fore wing; Upper Jurassic, USSR (Buryatskaya A.S.S.R.). Length of wing, 13 mm. After Martynova, 1961.

Fig. D. *Baissoptera koloznitsynae* Martynova, hind wing; Upper Jurassic, USSR (Buryatskaya A.S.S.R.). Length of wing 12.5 mm. After Martynova, 1961.

The Permian snake-flies are little-known.[1] *Sojanoraphidia* (Sojanoraphidiidae) from the Permian of the USSR (Marynova, 1952) has a long, curved ovipositor like that of the Recent species but the venation of the single wing that is known does not have the basic Raphidiodean pattern. It possesses a very long subcosta extending almost to the apex, and a very narrow costal space. What is most striking is the structure of the basal part of the radial sector and MA, which resembles the condition found in the hind wings of the Mesoraphidiidae, Alloraphidiidae and Baissopteridae. Although the apparent origin of this wing from the thorax indicates that it is a fore wing, as it was designated by Martynova, I find it difficult to believe that it is not the hind wing; at any rate, if it turns out to be the fore wing then quite clearly this is another very different line of the Raphidiodea from the others which are known in the fossil record. In fact, if it were not for the long, curved ovipositor, I would doubt that it could belong to the order.

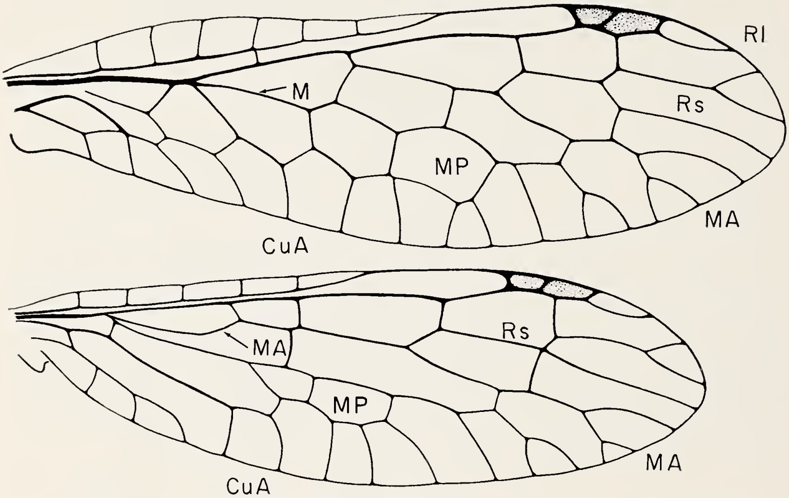


Figure 2. *Raphidia americana* Carpenter, fore and hind wings. Recent, Mexico (Carpenter, 1958).

I have serious doubts about the position of the families Lepalopteridae Martynova, from the Permian of USSR, and of the family

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[1] The family Permoraphidiidae Tillyard from the Lower Permian of Kansas is almost certainly not a snake-fly but most likely an orthopterous insect, related to the Permelcanidae and Oedischiidae.

Fatjanopteridae, from the Upper Carboniferous of USSR (Martynova, 1961). Neither of these families, each represented by a single species, seems to me to show in the wings the basic characteristics of the Raphidiodea. It is possible, of course, that like the Sojanoraphidiidae they could represent other radiating lines in the late Paleozoic, but they could equally well represent separate orders or suborders within the neuropteroid complex or, even, be members of the exopterygote series of insects. Until we know more of the wings and body structures of these insects, I consider their position uncertain even at the ordinal level.

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CRETACEOUS INSECTS FROM LABRADOR
3. A NEW GENUS AND SPECIES OF TERMITE. (ISOPTERA: HODOTERMITIDAE)[1]

By Alfred E. Emerson

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Introduction

The origin and dispersal of numerous higher taxa of termites by mid-Cretaceous times have been postulated from present geographical distributions and the existence of fairly advanced types in early to middle Tertiary deposits (Emerson, 1955, MSS). With the exception of a few extinct genera, the Oligocene termite fauna of Baltic amber includes several genera that are characteristic of present warm temperate climates of Europe and Asia. A recently discovered tropical termite fauna in Mexican amber of Oligocene-Miocene age is generically closely similar to the living fauna of the same region (Emerson, MSS). Heretofore, the earliest known fossil termites were found in Eocene deposits of North America, Australia, and Europe. The few specimens of Eocene age belong to the Mastotermitidae (Emerson, 1965) and Kalotermitidae (Emerson, MSS), but early Oligocene fossils from several deposits including Baltic amber belong to the Hodotermitidae, Mastotermitidae, Kalotermitidae, and Rhinotermitidae. The author and others have considered the fauna of Baltic amber to be of upper Eocene age (Emerson, 1955), but the general concensus now places this fauna in the lower Oligocene. The lack of the most advanced Termitidae from early Tertiary strata is probably due to the general scarcity or absence of this family in temperate climates in the northern hemisphere, and it is predicted that abundant fossils from tropical regions will prove the existence of numerous advanced genera of Termitidae in Cretaceous times. Indeed the tropical fauna of Mexican amber on the Oligocene-Miocene border proves the presence of living genera of various families that include the Termitidae at that time (Emerson, MSS).

The discovery of a fossil termite wing from late Early Cretaceous or early Late Cretaceous (Cenomanian) associated with a warm temperate flora in Labrador is a considerable extension of accurately determined specimens of the order Isoptera backward in geological

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[1] This investigation was supported by the National Science Foundation (Grant No. G-25146).

time. Earlier reports of fossil termites in Paleozoic deposits are all incorrect because of the erroneous assignment of specimens of other orders to the Isoptera. However, the author is of the opinion, admittedly speculative, that the Isoptera may have originated in early Mesozoic or even late Paleozoic times.

The single forewing here described is without doubt a termite. Only the Isoptera have a humeral suture at the base of the wing that enables the wings to be easily shed at the end of the colonizing flight. The deciduous wings are associated with the strictly social life of these insects, and this Cretaceous fossil is the earliest known social insect, inasmuch as the Labrador horizon is of an earlier age than the recently described fossil ants from Cretaceous amber of New Jersey.

Although the order may be determined accurately, a single forewing, although remarkably complete and well preserved, makes the assignment to other higher taxa somewhat more precarious. In the first place, the variation in the wing venation of species and genera of termites, particularly primitive termites, is great compared to the relative invariability characteristic of many other orders of insects. Wing venation alone cannot be used as confidently for taxonomic and phylogenetic interpretation of termites as it may be for other orders. Slight differences of wing venation, particularly of fossils, have often been interpreted as indications of species or generic differences that are obviously false when the variability of comparable living species is investigated. In the second place, fossils are always fragmentary and show a paucity of characters as compared to abundant series of all castes commonly collected from the living fauna.

In spite of the lack of other characters of the head, thorax, and abdomen, the author feels justified in assigning this forewing to the family Hodotermitidae, the subfamily Cretatermitinae, new subfamily, the genus *Cretatermes,* new genus, and the species *C. carpenteri,* new species. These taxa and their phylogenetic relationships must be considered as tentative working hypotheses until more abundant and extensive material is available for study and comparison.

Family Hodotermitidae Desneux

The present status of the Hodotermitidae is discussed by Emerson (in press). The distribution of fossil and living genera is interpreted by Emerson (1955, pp. 473, 482, 484, 490, 492, 498, 499, 502, 506, 507, 509, 516, 517).

The author has little doubt that *Cretatermes carpenteri* agrees with the wing venation of the Hodotermitidae. The wide area occupied by the radial sector (Rs) in the outer fourth of the forewing with the innermost branch joined to the inner margin near the wing tip (figs. 1, 2) is found only in some of the subfamilies of the Hodotermitidae. The relatively short cubitus (Cu) and the reticulations in the wing membrane between the veins are also in conformity with some subfamilies of the Hodotermitidae.

These combined characters of the forewing eliminate all other known families of termites. It should also be pointed out that this wing venation is associated with characteristic dentition of the imago mandibles, the lack of ocelli, more than two articles in the cerci, together with numerous other characters in more completely preserved fossils and living species of the Hodotermitidae. It is postulated (Emerson, in press) that an unknown ancestral group possessed the ocelli of the Mastotermitidae, Rhinotermitidae, and Termitidae, the dentition of the imago mandible close to that of *Archotermopsis* and the cockroaches, and a still more ancestral group probably possessed the anal lobe of the hind wing of the Mastotermitidae. Without preserved characters of the head, pronotum, legs, and abdomen of *Cretatermes carpenteri,* all that can be said at present is that this species most probably belongs to the Hodotermitidae. It is anticipated that this taxonomic assignment will be verified with the discovery of more specimens from the same deposit or of related species from other localities and strata.

Subfamily **Cretatermitinae**, new subfamily

In the early stages of this investigation, the author was loath to erect a new monotypic subfamily on the basis of a single fossil forewing, and he still has misgivings. However, he thinks that the tentative assignment to the new subfamily Cretatermitinae is the best nomenclatural and bibliographic symbol to handle the comparative data available. No other known subfamily of the Hodotermitidae has the combination of diagnostic characters illustrated in figs. 1, 2, and 3. These include: (1) the evenly curved humeral suture; (2) the greater length of the wing from the inner end of the humeral suture than from the costal end of the humeral suture; (3) the small size of the forewing; (4) the relatively wide wing in proportion to its length; (5) the gradual increase in the width of the area occupied by the radial sector (Rs) from the base to the apical fourth of the wing; (6) the branching of the media (M) in the basal fourth of the wing; (7) the position of the media (M) about half way between the radial sector (Rs) and the cubitus (Cu); and (8) the short cubitus (Cu) not reaching beyond the basal half of the inner margin of the wing. Some of these characters are shared with some genera of other subfamilies, but the combination does not fit any presently known subfamily of the Hodotermitidae.

The Termopsinae (Emerson, 1933, figs. 13, 30, 40) has a proportionately narrower area occupied by Rs in the outer portion of the wing; the length of the wing is considerably larger in all known species; the length of the forewing from the costal end of the humeral suture is about the same as or is shorter than the length of the forewing from the inner end of the humeral suture; Rs is roughly parallel to the costal margin; M is closer to Cu than to Rs in the middle of the wing; and the reticulations enclose smaller and more numerous spaces of the wing membrane.

The Hodotermitinae (Emerson, in press) has well defined inferior branches of Rs reaching the inner margin of the wing behind the tip; the humeral suture of the forewing is somewhat sinuate; the length of the forewing from the costal end of the humeral suture is about equal to the length from the inner end of the humeral suture. The characteristic inferior branches of Rs and the width of the area occupied by Rs and its branches in the outer portion of the wing allow rather easy identification of this subfamily from the forewings alone. It should be pointed out that there is only a little difference in the angles of the branches of Rs in designating a branch as inferior or superior, and in some individual cases the distinction is somewhat arbitrary. From an evolutionary point of view, the transition from superior to inferior branches would seem to be only a slight step, and some other subfamilies such as the Termopsinae, Porotermitinae, and Stolotermitinae have individuals that may have one or more inferior branches of Rs.

The subfamily Porotermitinae with a single genus including three species distributed in temperate areas of southern Australia, South Africa, and Chili, has a fairly straight humeral suture of the forewing with a short curve near the costal end; all known species of *Porotermes* are much larger than *Cretatermes*; the wing is proportionately longer compared to its width in most species of *Porotermes* except *P. adamsoni* in which the proportions are similar to those in *Cretatermes*; Rs is closely parallel to the costal margin throughout the length of the wing; the superior branches of Rs are thick and strong and are not secondarily branched as in the Cretatermitinae; the main stem of Rs is as strong as the superior branches, but from 0-3 inferior branches are as weak as M and reach the inner border of the wing below the tip; M is about half way between Rs and Cu in the middle of the wing or may be closer to Cu than to Rs; and Cu has from 5-12 primary branches, the longest extending from about half to four-fifths the length of the wing from the base. The reticulations of the wing membrane do not differ diagnostically from Cretatermitinae, and the inner margin of the wing of the Porotermitinae is longer than the costal margin from the suture in both subfamilies.

Sc, R_1, R_2, R_3, or R_{2+3} vary in the Porotermitinae and may not be diagnostically different from this obscure region of the forewing in the single fossil specimen of Cretatermitinae. In the Porotermitinae there may be as few as two branches of the radius emerging from the suture, or there may be a full complement of Sc, R_1, R_2, R_3, and Rs at the suture, thus illustrating the extreme variability of these veins in some species and genera of primitive termites.

In an occasional rather exceptional wing, M may have branches that invade the normal position of Rs, and in such cases the superior branches of M may be as strong as those of Rs and may also reach the costal margin of the outer portion of the forewing. Again, this illustrates the great variability of the venation of these primitive termites and the difficulty of making definitive comparisons. In spite of this degree of variation, however, the general pattern is sufficiently correlated with other characters to indicate valid taxa from the species to the family.

The Stolotermitinae is a subfamily based upon a single genus with six described species, one from temperate South Africa, one from New Zealand, one from Tasmania, one from temperate southeastern Australia, and two (possibly only one) from tropical eastern Australia.

The dentition of the mandibles of *Stolotermes* is of a very primitive type with strictly homologous teeth to those of cockroaches (Ahmad, 1950), and is only slightly advanced in a few particulars from that of *Archotermopsis* (Termopsinae) and *Ulmeriella* (Hodotermitinae). The reticulations of the forewing are not diagnostically different from *Cretatermes*; the humeral suture of the forewing is fairly straight or convexly curved in contrast to the concave curve of the humeral suture of *Cretatermes* (fig. 3); the humeral suture slants backward at a sharp angle from the costal to the inner margin; the veins from Rs to Cu are bent or curved down toward the inner border near the suture (Hill, 1942, fig. 1); the costal margin of the forewing is much shorter than the inner margin from the humeral suture to the tip; the shape of the wing may be similar to that of *Cretatermes* or a little longer compared to width; the linear length of the forewing is longer in all species of *Stolotermes* except *S. africanus* Emerson in which it may be slightly shorter than in *Cretatermes carpenteri*; Sc is short; R_1 is present and is occasionally branched; R_2 and R_3 are absent; Rs is gradually wider in the area occupied from the humeral suture to the outer portion of the wing, but is not so proportionately wide as in *Cretatermes* (figs. 1, 2); the superior branches of Rs are closer to each other with less width between them than in *Cretatermes*; Rs may have from 0-2 weaker inferior branches reaching the inner margin near the tip; M is long, not quite reaching the tip of the wing but with the lower branches reaching the inner margin about 1/3-3/5 the length of the inner margin from the suture; the first branch of M may be close to the suture as in *Cretatermes*; M is usually weaker than Rs and is usually closer to Cu than to Rs; Cu is usually short with 3-7 branches close together, the longest branch reaching the inner margin from 1/6 to nearly 1/2 the length of the wing (differs among species). The arolium is absent in the Stolotermitinae, Porotermitinae, and some Hodotermitinae and is present in the Termopsinae and some Hodotermitinae.

The major distinctions between the forewings of *Stolotermes* and *Cretatermes* are the shape and position of the humeral suture and the width of the area occupied by Rs and its superior branches about 3/4 the length of the wing from the base.

It is the opinion of the author that the forewing of *Cretatermes* is closer in more characters to the forewing of various species of *Stolotermes* than to other subfamilies, and resembles *Porotermes* next most closely. However, the resemblances and differences of a single forewing are insufficient to warrant any firm conclusion concerning the phylogenetic relationship between the Cretatermitinae and either the Stolotermitinae or the Porotermitinae other than to state that *Cretatermes* is advanced in its small size, the shape and position of the humeral suture, and in the relatively large spaces between the reticular thickenings of the wing membrane.

PHYLOGENETIC RELATIONS BETWEEN THE SUBFAMILIES OF THE HODOTERMITIDAE

There would seem to be little doubt that the more primitive genera (*Termopsis, Archotermopsis*) of the Termopsinae are the most primitive members of the Hodotermitidae, and in several particulars are the most primitive known termites (Emerson, 1933).

Recently (Emerson, in press) a redescription of the fossil genus *Ulmeriella* of the Hodotermitinae indicates that it is related to but is slightly more advanced than *Archotermopsis*. The various characters of *Ulmeriella* seem to be derived directly from primitive Termopsinae.

The Stolotermitinae has a very primitive left mandible of the imago (Ahmad, 1950; Emerson, 1942, 1947), but is derivative in numerous other characters, particularly in the sharply slanting humeral suture of the forewing. L. R. Cleveland discovered that *Stolotermes* is the only genus of termites that shares a genus of wood-ingesting intestinal flagellates with the wood-feeding cockroach, *Cryptocercus* (see Emerson, 1961, for a discussion of the evolutionary implications of this discovery). The Stolotermitinae could have branched off from primitive Termopsinae or possibly from primitive Hodotermitinae, but could not have the Porotermitinae in its ancestry as that subfamily is now conceived, primarily because the Porotermitinae has a much reduced second marginal tooth of the left mandible. The Porotermitinae could not be derived from the Stolotermitinae because of the advanced type of humeral suture in the latter subfamily, but it could have branched off from the less primitive Termopsinae or possibly from the Hodotermitinae although only before the specialized harvester behavior had evolved.

Because of the less advanced type of humeral suture, the forewing of the Cretatermitinae could not have arisen from the Stolotermitinae which it resembles in some characters. The wing of the Cretatermitinae might be related remotely to the Porotermitinae, but the data are insufficient to enable us clearly to separate homologous from analogous characters, and parallel reduction from homologous reduction. With more characters of the species available, it may be possible to find consistent patterns of phylogenetic importance, but at present it is necessary to state that several alternative hypotheses of phylogenetic derivation could account for the meager facts. The small size of *Cretatermes* is reasonably certain to be derivative, but the small size of *Stolotermes africanus* could have arisen independently, each from more primitive groups of larger size.

With our present information, the Hodotermitidae consist of fossil and living relicts that are spotty and often discontinuous in their distribution. The Porotermitinae and Stolotermitinae, neither represented by known fossils, are found only in the southern hemisphere, and the genera are probably Mesozoic in origin and dispersal because of their existence on different continental masses long isolated from one another. The living and fossil Termopsinae are all found in the north warm temperate zones with a gradation from the most

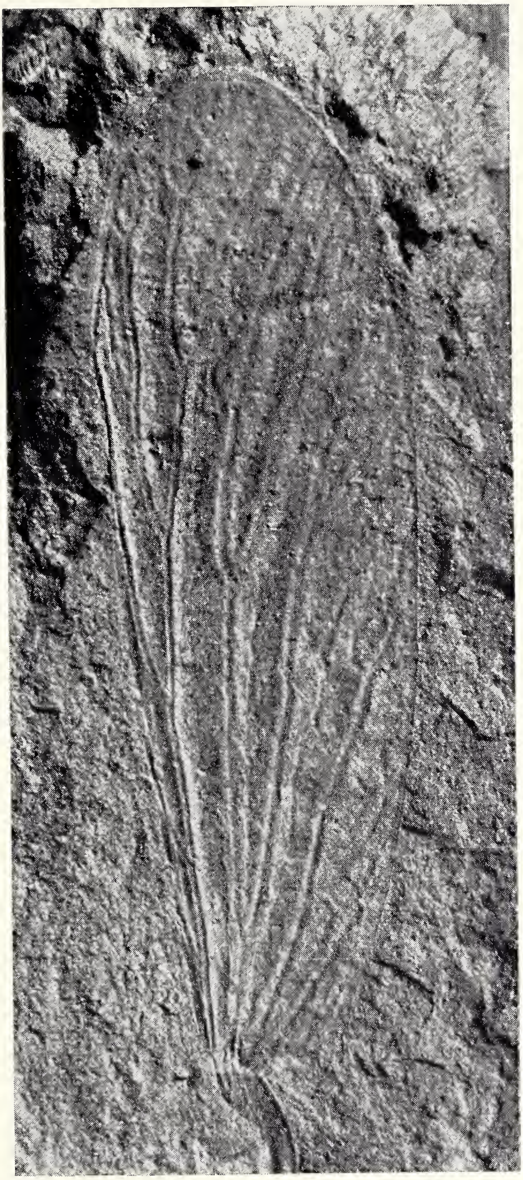

Fig. 1. Photograph of holotype forewing of *Cretatermes carpenteri*, new genus, new species.

primitive in Eurasia and the derivative genera in Tertiary and present North America. The only known fossil of the subfamily Hodotermitinae is *Ulmeriella* (Emerson, in press) found in Tertiary temperate deposits of Europe, Asia, and North America, while the living genera (3) of the Hodotermitinae are the desert and steppe harvester termites of temperate and tropical Africa and Asia. These distributions in time and space would seem to indicate a very ancient origin with considerable extinction of intergrades between the relict types of fossils and present survivors (Emerson, 1955, in press).

Cretatermes now provides direct evidence of the existence of a fairly advanced subfamily of the otherwise primitive family of Hodotermitidae in mid-Cretaceous times, and indicates that the origin of this family of termites and the order Isoptera is much earlier than the Labrador deposits. The author suggests that the origin of the Hodotermitidae may be Triassic and that the origin of the Isoptera may be late Paleozoic.

Genus **Cretatermes**, new genus

TYPE SPECIES: *Cretatermes carpenteri*, new species.

With only a single forewing representing a monotypic subfamily, and with no data on the variation within the species or the common characteristics of several species within the genus, the description of the genus and the subfamily coincides for the present.

From the knowledge of species and generic differences in the other subfamilies of Hodotermitidae, however, it is possible to indicate the characters that might be considered of subfamily rank and those that might be considered of generic rank.

The forewings of various genera of Termopsinae show differences in the shape of the humeral suture (Emerson, 1933) with very few differences in the wing venation beyond the suture.

Generic characters of the Hodotermitinae are found in the mandibles and the tibial spines, while the wings show little distinction.

The subfamilies of Porotermitinae and Stolotermitinae, each known from a single genus, show little variation of the humeral suture within each genus, and also show numerous generic characters of the wing venation. Smaller degrees of difference in the wing venation indicate species distinctions.

The species within the genera can often be distinguished by the shape of the wing, the relation of length to breadth, small differences in the shape of the humeral suture, and the mean sizes of male and female forewings and other structures. On occasion, specific variation in wing venation can be detected, although many wings must

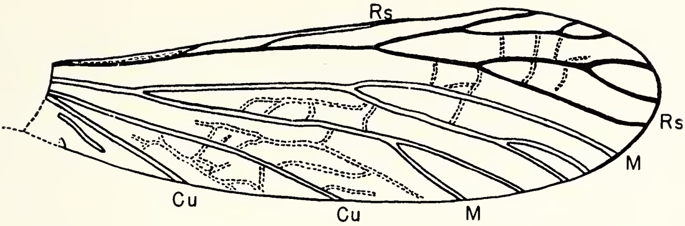

Fig. 2. Drawing of visible veins and reticulations of holotype forewing of *Cretatermes carpenteri*, new genus, new species. Rs = radial sector. M = media. Cu = Cubitus.

be examined because of the large degree of variation between individuals and even between the right and left wing of the same individual. For adequate species distinction, a set of head, thoracal, and abdominal characters that are correlated with the wing venation should be described, but unfortunately this is not yet possible for *Cretatermes carpenteri.* The following description, therefore, contains characters of various systematic categories from individual variation to subfamily distinctions, and we must await the discovery of more material and a more thorough study of variation at various related taxonomic levels before we can make taxonomic distinctions and find common qualities of each taxon. This does not mean that the author agrees with those who would eliminate the concepts of species and higher taxonomic categories. On the contrary, he finds the taxa with their shared homologous characters have distinctions that rest upon a wealth of demonstrated biological principles resulting from investigations in a variety of disciplines. Taxonomic and phylogenetic order can be discovered from abundant material subjected to a variety of observational and experimental techniques together with comparative cross-disciplinary studies (Emerson, 1961, in print, MSS).

Cretatermes carpenteri, new species

RIGHT FOREWING: General shape as in figs. 1, 2. The costal margin of the basal 10/13 of the wing is slightly convex; tip of wing rounded and about half way between the costal and inner margins; inner margin evenly convex, more curved than the costal margin.

Numerous thickenings or reticulations (archidictyon) of the wing membrane occur between the branches of Rs, between Rs and M, between M and Cu, and between the branches of both M and Cu. The enclosed spaces within the reticulum are large compared to those of the Termopsinae and Hodotermitinae.

Scale broken and the shape is not preserved. The costal margin that often shows important taxonomic distinction is broken off. Some veins seem to cross the humeral suture from the scale to the wing beyond the suture, but some strongly marked structures do not seem to fit the anatomy of the forewing scale and may be other structures separate from the wing that impinge upon it in the preserved scale, or else are marks in the rock.

Humeral suture (fig. 3) seems to be reasonably well preserved. It is evenly curved and slants backward toward its junction with the inner margin. The inner portion of the suture is not as clear as the costal end, but the extension of the clear edges of the suture and the inner margin seem to indicate the true shape and position of the inner portion of the suture. The suture is not angulate in the region of Rs. The inner margin of the wing is somewhat concave where it joins the suture.

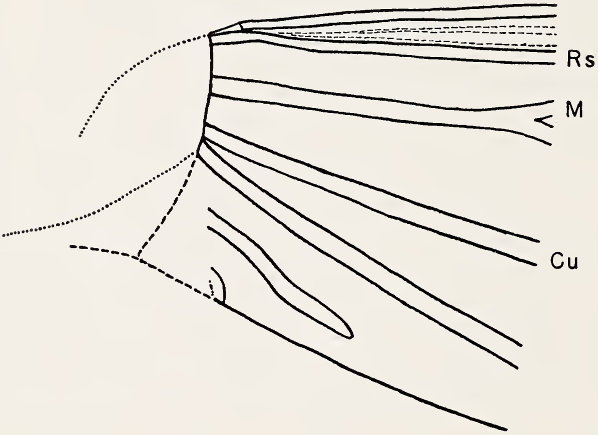

Fig. 3. Drawing of base of holotype forewing of *Cretatermes carpenteri*, new genus, new species, showing visible veins emerging from the humeral suture.

The veins that emerge from the suture at the costal margin (fig. 3) are somewhat obscure and the wing in this region is either broken or folded. Sc is not clearly visible although it is probably present in well preserved wings. What seems to be the costal margin at the suture may possibly be R_1 with the actual costal margin either broken or folded under. There are indications of veins between the costal edge and Rs, and it is possible that R_1 and R_{2+3} are present. These veins vary considerably in some genera of Hodotermitidae. A vein joins the costal margin about 1.22 mm. from the suture but it is not clear whether this is the first superior branch of Rs or the end of one of the other branches of the radius. Clear superior branches of Rs occur about 2.63 mm., 3.88 mm., and 5.08 mm. from the suture, and secondary and tertiary branches occur in the apical fourth of the wing. The main stem of Rs ends well below the tip of the wing. In summary, seven and possibly eight branches of Rs reach the costal margin and tip of the wing. The width of the radial sector (Rs) and its branches in the outer fourth of the wing (figs. 1, 2) and the gradual divergence of the main stem of the radial sector from the costal margin are interpreted as generic and subfamily characters. The branches of Rs are more defined and are narrower than those of M and Cu. M branches into an upper and lower branch about 1.01 mm. from the suture, somewhat closer to the suture than in most termites, but the taxonomic significance cannot be interpreted without many more specimens. Five branches of M reach the lower margin in the apical half of the wing, but this character is almost surely variable within the species. The general position of M about half way between Rs and Cu is probably of generic importance and might even be of species importance. Cu is comparatively short, its longest branch ending close to the middle of the inner margin. The length of Cu is probably of species or generic importance. Cu and M emerge from the suture in a fan-like spread of veins, in this particular strikingly different from the sharply curved veins of *Stolotermes.*

MEASUREMENTS OF THE FOREWING OF CRETATERMES CARPENTERI, NEW SPECIES

Length of suture from costal to inner margin about	0.72 mm.
Length of wing from costal end of suture	7.23 mm.
Length of wing from inner end of suture	7.42 mm.
Width of wing	2.23 mm.
Widest width of radial sector	0.93 mm.
Width between Rs and M near middle of wing	0.39 mm.
Width between upper and lower branches of M in middle of wing	0.37 mm.
Widest width between M and Cu about 1/3 length of wing from suture	0.44 mm.

SPECIMEN: Holotype, right forewing and counterpart impressions, of Cenomanian age, at the border between Lower and Upper Cretaceous, in a bed of hard ferruginous argillite associated with rubble ores at the Redmond No. 1 deposit near Schefferville (latitude 54°50′ N., longitude 67°00′ W.) in the Knob Lake district, Labrador; collected by Professor Erling Dorf. The holotype is No. 87270, Invertebrate Paleontology collections, Princeton University. From associated fossil plants, Dorf (1959) suggests that the climate at the time of preservation was warm temperate.

ACKNOWLEDGEMENTS

The author is indebted to Frank M. Carpenter of the Biological Laboratories, Harvard University, for making the specimen available to me and for his numerous critical comments through many years on various aspects of insect paleontology. The author also wishes to thank his wife, Eleanor Fish Emerson, for her valued assistance in the preparation and editing of the manuscript.

SUMMARY

The earliest known specimen of a termite (Isoptera), that is also the earliest known fossil of a strictly social insect, is described and figured from a forewing from mid-Cretaceous deposits near Schefferville, Labrador. The forewing is classified as *Cretatermes carpenteri*, new genus, new species, and included in the subfamily Cretatermitinae, new subfamily of the family Hodotermitidae. Systematic and phylogenetic interpretations and comparisons are included.

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SPECIES OF WIDOW SPIDERS IN NORTHERN ARGENTINA (*LATRODECTUS:* THERIDIIDAE)

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Harvard University

INTRODUCTION

For more than fifty years there has been considerable controversy over the number of South American species in the genus *Latrodectus*. In a recent study Gerschman de Pikelin and Schiapelli (1965) reported that *Latrodectus* is represented by only two species, *L. geometricus* (Fabricius) and *L. mactans* C. L. Koch in Argentina. They opposed the findings of Abalos (1962), who suggested that at least five species of *Latrodectus* occur in Santiago del Estero, a northern province of Argentina. In addition to *L. geometricus,* Abalos proposed that four distinct species, temporarily designated No. 1, No. 2, No. 3 and No. 4, comprise the *mactans* complex; whereas, Gerschman de Pikelin and Schiapelli believe that these four species ". . . . cannot be maintained because they are based only in the small differences in the form and size of their egg-sacs". Abalos and Baez (1967) supported the original findings of Abalos with additional ecological and morphological data. The present paper is concerned only with the four sympatric populations placed by Abalos and Baez into the "*Latrodectus curacaviensis* group" (No. 1) and the "*Latrodectus mactans* group" (Nos. 2, 3 and 4).

I would like to acknowledge with sincere thanks the constant advice and encouragement by Dr. H. W. Levi of the Museum of Comparative Zoology and the loan of material by Dr. J. W. Abalos of the University of Córdoba, Córdoba, Argentina. The study was supported in part by Harvard University and by Public Health Service Research Grant AI-01944 from the National Institute of Allergy and Infectious Diseases.

METHODS

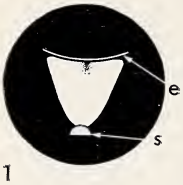
In suggesting that the "*curacaviensis-mactans*" complex was comprised of four species, Abalos relied heavily upon field observations made in Santiago del Estero. On the other hand, Gerschman de Pikelin and Schiapelli relied mainly upon their studies of the morphological variations of specimens collected throughout Argentina and at least two neighboring countries. In order to minimize the problem of geographical variation within species, I limited my study to specimens collected in the small region sudied by Abalos. Furthermore, the study specimens were recently captured adult females which were preserved in a uniform manner. This was intended to reduce the problems resulting from ageing, e.g. differential fading and shrinking. Males were unavailable in sufficient numbers and were excluded from this study.

I would like to point out that Gerschman de Pikelin and Schiapelli noted variations in the size and color of the successive egg sacs from a single female. After examining the same egg sacs, Levi (pers. comm.) attributed the color variation to an unequal accumulation of dust on each of the egg sacs.

In a review of some North American *Latrodectus,* McCrone and Levi (1964) noted the distinct difference in the ventral abdominal patterns between *L. mactans* and *L. variolus* Walckenaer. This led me to study these familiar markings between the epigastric furrow and spinnerets. After examining several abdomens, I found that a few basic patterns were present on a majority of the specimens. These basic patterns and all variations of the basic patterns were sketched with the aid of a dissecting microscope equipped with an ocular grid. In this manner, the patterns from 266 specimens were compared.

In alcohol the red and yellow-brown pigments fade or wash out and as a result all pattern colors appear yellow or reddish-yellow. But there was a distinct difference between the color of the preservative of population No. 2 and the preservative of the other populations. The solutions from the vials containing No. 2 were tinted a deep orange while the preservative from the vials containing Nos. 1, 3 and 4 was usually colorless or rarely tinted with yellow. In order to obtain reproducible spectra from each of the species, Dr. Abalos sent additional specimens of Nos. 1, 2, and 3 which were preserved in alcohol. Additional specimens of No. 4 were unavailable. Upon receipt, each spider was washed in distilled water and 95% ethanol; the abdomen was divided along the mid-frontal plane; the internal organs and tissues of the ventral portion were excised; the exoskeletons were weighed and placed in separate vials containing equivalent proportions (weight/volume) of 80% ethanol. The vials containing the samples and vials of normal solutions (80% ethanol to be used for calibration) were sealed with polyethylene caps and stored for 14 months. This method was designed to provide uniform samples for analysis. With a Bausch & Lomb Spectronic 20 spectrophotometer measurements were made at 5 nm intervals between 380 and 650 nm.

The solutions were used without purification or dilution, except where noted. Although the color of the solution was probably due



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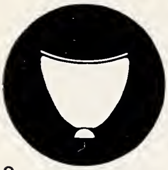

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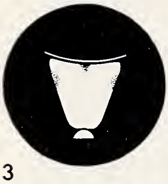

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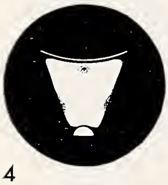

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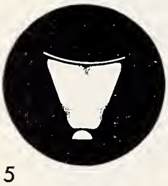

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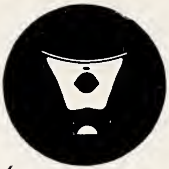

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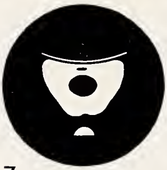

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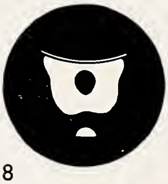

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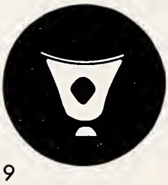

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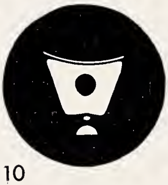

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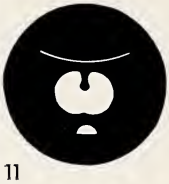

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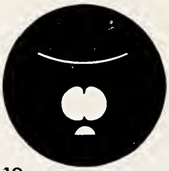

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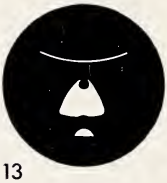

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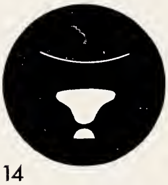

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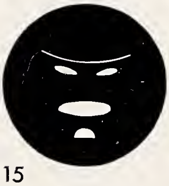

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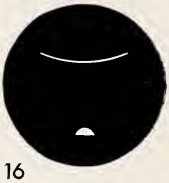

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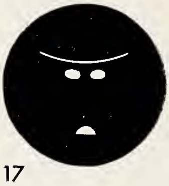

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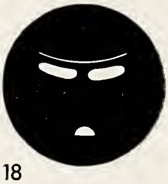

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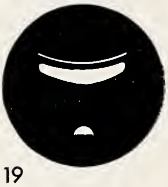

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PINTER — LATRODECTUS

to non-melanin pigments, no attempt was made to identify the pigments. They are assumed to be ommochromes.

With the use of an ocular micrometer, accurate to 0.1 mm, measurements were made of 34 morphological features. These measurements were selected because the margins of the structures were readily determined, thus permitting precise measurements which can be duplicated. The measurements taken between the eyes were not used because there were no significant differences between the individual species. Some ratios obtained from the remaining values are illustrated (Fig. 25) and discussed.

Using the dissecting techniques described by Levi (1965), I removed the epigyna from the specimens and exposed the internal genitalia by removing associated tissue and clearing the ducts in clove oil. Illustrations were made of the seminal receptacle, and the external and internal duct spirals (according to de Biasi, 1962).

RESULTS

Abdominal markings. A variety of ventral markings are shown in Figures 1-19.

The vertical columns of venter patterns illustrate some of those observed in each of the populations.

In population No. 1, the yellow pattern had a shield-like appearance. There were two specimens with complete shields which filled the ventral area (Fig. 2) and a few specimens had shields with indentations along the anterior or lateral margin (Figs. 3, 4 & 5), but the majority of the shields had only a faint black indentation along the anterior border (Fig. 1). With no exception among 83 specimens, the shield extended from the margin of the epigastric furrow to the base of the spinnerets; whereas, there were no examples of this feature among the specimens from the other three populations.

In population No. 2 a slightly different pattern emerged. Whereas the pattern did not extend posteriorly to the spinnerets, the entire anterior margin of the square was in contiguity at the epigastric furrow on all (136) specimens. Figures 6 through 10 show five variations of the basic square pattern; a majority of the patterns were similar to that shown in fig. 8. In studying a much larger

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EXPLANATION OF PLATE 36

Figs. 1-19. Abdominal Markings. Diagrammatic illustrations showing the ventral abdominal patterns, including the epigastric furrow (e) and spinnerets (s); booklungs, epigyna, and lateral extensions of the dorsal pattern are not shown. 1-5. *Latrodectus* No. 1. 6-10. *Latrodectus* No. 2. 11-15. *Latrodectus* No. 3. 16-19. *Latrodectus* No. 4.

sample, Abalos and Baez also observed this fact because they noted that the red irregular square stretched "... almost to the spinnerets". A more conspicuous feature was the presence of a circular black spot in the center of the square. The presence of a round black spot, centered in a reddish yellow irregular square, was sufficient to distinguish specimens of population No. 2 from all other specimens.

Any attempt to characterize the faded yellow patterns observed in populations Nos. 3 and 4 becomes hazardous. No two patterns were alike in either of the two populations. The majority of the specimens from No. 3 had patterns similar to those illustrated in Figures 11 and 12. The pattern edges were less distinct than those seen in Nos. 1 and 2. It is interesting to note that when McCrone and Levi (1966, p. 182) state "... the use of color pattern as a diagnostic species character must be done with great caution", they were probably studying the Peruvian counterpart of population No. 3. This variability is equally true of population No. 4, of which only four specimens were available for study. All four patterns are illustrated (Fig. 16 through 19). More specimens need to be studied before one can be reasonably certain that the yellow markings were restricted to the anterior portion of the venter.

Color. The pattern colors of Nos. 1, 3 and 4 varied from dull to brilliant yellow, while those of No. 2 varied from dark red to reddish-yellow. But the colors of the preservatives were of more interest to me than the colors of the patterns. It was obvious that the preservative for No. 2 was tinted with a red pigment and the preservatives for Nos. 1, 3 and 4 were colorless. Using the technique described earlier, the absorption curves of the preservatives of Nos. 1, 2 and 3 were measured and plotted and a comparison of the curves in Figure 20 shows the dramatic difference between the undiluted samples (see unbroken curve in Fig. 20). Following a 4:1 dilution of the solution from population No. 2 (lowest curve), the spectral curve (dotted line) moved into the absorption range of the other samples. Undoubtedly, the same pigments are present in all three populations. In comparison with No. 3, one might suggest that the greater amount of dissolved pigments in No. 2 resulted from the larger pattern in No. 2. But it might be possible that the red and yellow pigments (non-melanins) are not necessarily limited to the pattern areas and are present in the black (melanin) pigmented areas as well. This argument becomes less important when comparing No. 1 to No. 2. Indeed, the area covered by the shield (No. 1) is greater than that of the square (No. 2). Therefore, the greater intensity of red pigments in the preserving solution probably resulted from a greater abundance of soluble pigments in the ventral abdominal integument of No. 2 than in Nos. 1 or 3.

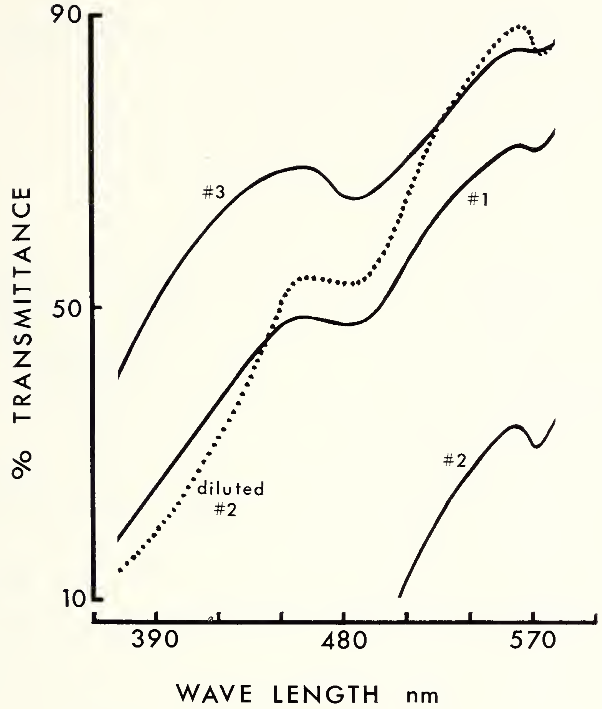
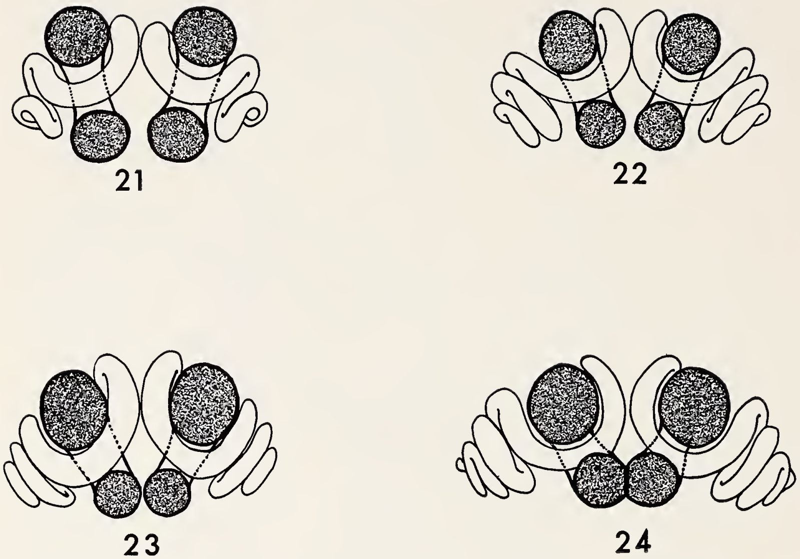


Fig. 20. Color. Spectral curves of pigments of *Latrodectus* Nos. 1, 2 and 3.

Internal Genitalia. The importance of studying the internal variations of the female genitalia of theridiids has been repeatedly stressed by Levi (1959, 1962 & 1965). The basic structural difference in the number of coils of the duct is illustrated in Figures 21 through 24. No. 1 can easily be distinguished on the basis of one and a half to two turns of the duct. Figure 21 illustrates a duct with one and three-quarter turns. This compares with that of No. 1 of Abalos and Baez (p. 63). In the other populations the ducts are more complex. In Nos. 2, 3 and 4 the ducts make approximately three complete turns. In the four specimens of No. 4 the ducts make an additional quarter turn. One might best describe this situation as three and one-



Figs. 21-24. Internal genitalia. Cleared dorsal view of epigyna. 21. *Latrodectus* No. 1. 22. *Latrodectus* No. 2. 23. *Latrodectus* No. 3. 24. *Latrodectus* No. 4. All figures are drawn to the same magnification.

quarter turns. Although No. 4 appears to have the most convoluted duct system, it would be necessary to examine more specimens before I could suggest that the quarter turn is signficant. Unfortunately, Abalos and Baez limited their characterization of the internal genitalia of Nos. 2, 3 and 4 to a single illustration (p. 63) which represents the duct system found in all three populations.

Measurements. A series of 34 measurements were made on a variety of external parameters on 94 specimens (30 specimens from populations Nos. 1, 2, and 3; and four specimens from No. 4). After an analysis of all the values for each of the populations, the measurements from some parameters were discarded because they failed to yield normal distributions, e.g., values for the epigynal width yielded a bimodal distribution for population No. 3. Values for the sternum width produced a distribution which closely approximated a normal curve. Two ratios were made with the values of the sternum width and two other measurements which were selected at random from the list of remaining measurements. A third ratio was made by pairing the values of two parameters selected at random. Modified Dice-Leraas diagrams for the ratios (FemurI/Sternum width, Metatar-

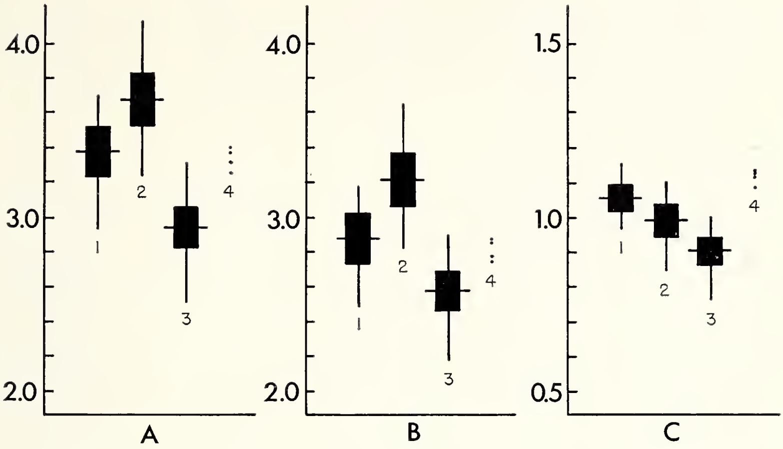


Fig. 25. Measurements. Ratios of *Latrodectus* Nos. 1, 2, 3, and 4. Modified Dice-Leraas diagrams of the ratios of Femur I/Sternum width (A), Metatarsus IV/Sternum width (B), and Femur I/Patella-tibia I. The horizontal line denotes the mean, the rectangle indicates the 95 per cent confidence intervals for the mean, and the vertical line represents the observed range. N equals 30 for *Latrodectus* Nos. 1, 2 and 3; N equals 4 for *Latrodectus* No. 4.

sus IV/Sternum width, and Femur I/Patella-tibia I) and the individual ratios for the four specimens from population No. 4 are illustrated in Figure 25.

The t-test was applied to the differences between the means of each of the ratios for each of the three populations. With a comparison of any of the three ratios, one finds a statistically significant difference (.95 confidence) between populations No. 1 and No. 2, No. 1 and No. 3, and No. 2 and No. 3.

CONCLUSION

By failing to consider geographic variation, Gerschman de Pikelin and Schiapelli confused a number of species. Their conclusion may be rejected on the grounds that there is reasonable evidence to conclude that at least three, and probably four, species besides *L. geometricus* are present in Santiago del Estero, Argentina. Because this study was limited to sympatric species, it was possible to show that a morphological discontinuity exists between the populations, hence reproductive isolation. These results support the findings of Abalos and Baez.

Because more work needs to be done on individual, as well as geographical, variation of the several species of South American *Latrodectus,* no attempt was made at this time to determine the names of species Nos. 1, 2, 3, and 4 from Santiago del Estero, Argentina.

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SLAVE-RAIDS OF THE ANT *POLYERGUS LUCIDUS* MAYR*

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Since slave-making raids of the genus *Polyergus* are conspicuous and spectacular, they have been studied by a number of myrmecologists. Among these are Wheeler (1910), Forel (1928), Creighton (1950), and Dobrzanska and Dobrzanski (1960). This paper concerns the eastern "shining slave-maker," *Polyergus lucidus* Mayr, on the Edwin S. George Reserve in southeastern Michigan (Livingston County). Twenty-five colonies of this species have been found, scattered quite widely over the fields, on the 2 square miles of the Reserve. Most of the fields tend to be dry, with Canada bluegrass (*Poa compressa* L.) the dominant grass and with forbes such as wild bergamot (*Monarda fistulosa* L.) bush-clover (*Lespedeza virginica* (L.) Britt.), and goldenrod (*Solidago* spp.) common and characteristic. In addition to this main habitat, *Polyergus* colonies may sometimes be found at woods' edge, in low wet fields, and in openings in oak-hickory woods where blueberries (*Vaccinium angustifolium* Ait.), bracken (*Pteridium aquilinium latiusculum* (Desv.) Underw.), sedge (*Carex pennsylvanica* Lam.), and mosses are characteristic. No colony has been found completely within the woods, although the slave ant *Formica pallidefulva nitidiventris* Emery sometimes occurs there.

The slave-raid study was undertaken in the hope of determining the time of day of raids and the environmental factors which influence the time, the days on which no raids occur and the factors which determine this absence, the number of slave colonies used in the support of one *Polyergus* colony, the distances to these colonies and the amount of time it took to reach them, the number of raids in a season, the number of brood taken, the size and characteristics of a raiding force, and the method by which the band of ants could travel over a seemingly unknown path to arrive exactly at a nest to be raided.

Preliminary studies were made on the Lawn Colony, which lived in the cut grass outside the East Gate Laboratory and had been known

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to exist there for 10 years (1956-1965); but the main observations concerned a larger colony, located about a mile away on grid 0-26 and known since 1961. Raids of this colony were recorded during two seasons. In 1964, during 50 days of observation in June, July, August, and early September, 29 raids were seen; and in the summer of 1965, during 54 days of observation, 34 raids took place.

NEST STRUCTURE AND COLONY SIZE

The structure of the compound nests seemed typical of the slave species *F. p. nitidiventris*, which usually dig a shaft into the ground and then excavate chambers from it at various levels. Shafts may be single or multiple and may extend as deep as 3.5 ft. Entrances to the nest (occasionally there are 2 to 5) may be inconspicuous in the grass or may be surrounded by bare excavated soil.

On August 30 and September 1 (it rained all day August 31) of 1965, one *Polyergus lucidus-Formica pallidefulva nitidiventris* mixed colony was dug. This nest lay near the top of a grassy slope in the sandy loam which is common on the Reserve. To judge by a raid seen on July 19, 1965, in which 258 workers took part, it was a medium-sized colony. Thirty-seven chambers were found, extending down to 30 inches and spreading around the central opening for a radius of 8 inches. Because of the lateness of the season, there were no larvae or eggs in the nest; and some of the winged ants had already flown. The *Polyergus lucidus* population consisted of one queen, 291 workers, 299 worker pupae, 115 females, 407 males, and 13 male pupae. The *F. p. nitidiventris* numbered 4,527 workers and 9 worker pupae. Thus the mixed colony contained approximately 5,662 individuals, and the count of 590 *Polyergus* workers (adult and pupae) gave a ratio of 7.7 slaves to each *Polyergus* worker.

TYPICAL RAID ACTIVITIES

The 0-26 colony had an almost bare nest area 18 × 18 inches across, because I had dug into it early in 1964. Generally there was only an occasional ant in sight here during the morning and none during the warm midday period. By early afternoon 2 to 5 *Polyergus* could often be seen circling about or running off into the surrounding grasses. Later, as the sun slanted to the west and the nest came into flickering shade, more ants came out and stayed on the nest area, circling and crossing it in a zigzag running movement. Then, typically, there would be an outpouring of ants until they covered the nest. As they milled about, they explored into the surrounding grasses for several inches. Gradually the group would begin to favor one side, pushing into the grasses a little farther but always running back and forth. Sometimes they retreated from one place to gather at another. The actual beginning of a foray was not certain until a line of ants extended a foot or more from the nest. Once a trail began, ants drained off from other parts of the nest so gradually that the front line might be as far as 8 feet away before the last got started; but soon the ants condensed to a group 2 to 4 feet long and 6 to 8 inches wide. Once a raiding column was formed, it moved fast — about 3 feet a minute — but always the ants alternated running back and forth and from side to side with the forward movement, so there were never any consistent leaders to the group.

The speed and compactness of the column was usually maintained, but sometimes the column widened to 10 or 12 inches, especially when loose leaves were being investigated. But, while a few ants might search for openings along the way, the main column kept moving steadily forward with no hesitation, following what seemed to be an obvious trail to a definite objective. Usually they arrived precisely at a nest to be raided. Sometimes they missed it by 2 to 10 inches. Once the spot was reached, all of the ants began searching every crevice in a frenzied fashion until the nest entrance was found. If the compact mass of workers did not find the entrance immediately, they began spreading out in widening circles. If the located entrance was open, they poured down it; if it was barricaded with pebbles and soil, they might dig for as much as 3 to 7 minutes before gaining admittance. Most of the *F. p. nitidiventris* colonies in the raided area kept their nests barricaded. Workers usually did not try to defend the nest, nor did they take away brood. Sometimes a worker was carried out and released; sometimes one ran out by itself, but there was seldom any fighting. Once the *Polyergus* gained entrance to a nest, it was only a minute or two until an ant reappeared carrying a pupa or larva. Others followed quickly, carrying out loot and starting for home. They returned by the same general path that they had taken in coming, each ant picking its own way over a 5- to 10-inch width. At home the ants entered the nest with their brood (at the Lawn Nest they sometimes piled it up for the *F. p. nitidiventris* workers to carry down).

When conditions were right, a second raid would take place. Sometimes the second column started before all the first ants had come in; sometimes there was a delay while they milled about the nest. Occasionally the second raid began with ants pouring out of the nest after all had gone below ground. On rare occasions a third raid took place; and once, after a successful raid, 2 columns started out in different directions at exactly the same time.

MEANS OF LOCATING COLONIES TO BE RAIDED

Polyergus raids were definitely not exploratory forays. There was no set pattern of pathways. The ants went directly to the nest to be raided (except that they might follow a contour of the land), and a nest visited twice on different days might be approached by quite different routes. This suggested that individual ants do the scouting and locating of colonies. This was verified, to my satisfaction, during the study. Observations made on July 6, 1965, gave an especially clear picture. During that morning an occasional *Polyergus* worker appeared on the surface; but between 11:15 AM and 2:55 PM none came out, although the temperatures were not especially high (81°-85°F 10 inches above the surface and 91°-95°F on the surface). At 2:55 PM 3 workers emerged, moved huriedly across the bare soil and disappeared into the grasses. For the next 40 minutes there were one or 2 *Polyergus* on the nest area at all times, and at least 10 of these slipped off into the grasses. Gradually more *Polyergus* joined those on the nest until there were 3 to 10 running about, and 2 per minute left the nest until 4 PM. After that time most stayed on the nest and only a few left, but in the whole time from 2:55 PM to 4:15 PM 52 ants were seen to depart. During this time none returned. Then at 4:15 PM a *Polyergus* was seen 3 feet from the nest, coming directly home. It went into the nest entrance, and within a few seconds a whole stream of ants began pouring out. They spread thickly over the nest area and within 5 minutes had started a raid to the west where the scout had come in.

On other days the departure of scouts was less conspicuous, and seldom was one lucky enough to spot a scout coming in. But whenever an ant came in hurriedly from the grass and went directly into the nest, there was an outpouring of ants. It was thus assumed that whenever a sudden emergence occurred it was in response to a messenger arriving with news of a located colony. If this was correct and if the scouting ant, which found a colony, laid down an odor trail on its way home, then the odor must have been quite long lasting, for it sometimes took an ant 30 to 45 minutes to return from a raided nest. It seemed unlikely that a raiding group could be following anything but an odor trail, for it moved rapidly, did not maintain leaders, and usually stopped at exactly the right place.

In contrast to raiding activity, which seemed mechanical and stereotyped, activities of workers while scouting for colonies must require a high degree of individual action and response to the configuration of the surroundings, which results in the ability to come home directly after a nest is found.

Experiments made in 1966 and 1967 seem to verify the odor-trail theory. On August 16, 1966, 10 *Polyergus* workers from nest 0-26 were crushed in dichloromethane to extract pheromones. Next day the colony was visited at 3:30 PM when early preraid activities were beginning, with a dozen *Polyergus* circling about the nest area and surrounding grasses. A pheromone trail, laid down with a small brush, was extended from the nest for 3 feet. Instantly ants began to follow the brush; and by the time the trail was complete, 50 ants were upon it. More came from the nest, and in 5 minutes there were about 75. Each ant ran forward and backward and from side to side, crossing and recrossing the odor trail, just as they did on their own raiding trails. At trail's end they ran forward and to each side, as they did when one of their own trails ended without leading to a nest. Then, finding nothing, they began to return home; and in 25 minutes all but 10 had abandoned the trail. There had been no outpouring of ants from the nest (the odor trail began at nest edge), and ants did not mass in a typical raiding formation. But each ant, going singly on the trail, had acted in characteristic fashion.

The same pheromone solution was then taken to another colony (M-26), which had ants out in preraiding activity at 4:23 PM. A trail 6 feet long was made; and again ants followed the brush immediately, moving back and forth and from side to side along the trail. In this case about 100 ants were attracted. Again they came along the trail singly, explored a little beyond it, and returned when no nest was found.

On August 20, 1966, a trail was attempted under conditions when no ants would normally be out. A dichloromethane solution of 10 crushed ants from M-26 was used. The *Polyergus* colony was visited when it was still in hot, bright sun. No *Polyergus* were in sight until the nest was shaded. Within 10 minutes about 25 *Polygerus* were running about, keeping in the shade. A short trail, stretching 12 inches out onto the hot soil, induced those crossing it to follow; but they came back almost immediately. Subsequent trails were extended out in different directions for 4, 7, and 11 feet. In each case ants followed these trails, although the soil was still hot enough to prevent ordinary raids.

It was found that dabs of solution worked as well as a continuous line, since ants found them readily as they zigzaged back and forth. Putting the brush into the nest entrance caused 25 to 30 ants to come out, but those which the brush touched were injured by the dichloromethane. Although there was great excitement on the nest, at no time was there any organization into a raiding mass; instead, each ant followed the trail singly. A dichloromethan solution made with *F. p. nitidiventris* workers caused no reaction at all.

On July 6, 1967, a successful raid on *F. pf. nitidiventris* was induced. Several days previously part of a colony had been dug and placed in a transparent plastic shoe box with a door made at one end. Workers excavated cavities in the soil and established their brood there. The box was placed 6 feet from nest M-26, and the *Polyergus* entrance was watched until ants began coming out. When there were 25 to 30 *Polyergus* circling the entrance (4:20 PM), the *F. p. nitidiventris* door was opened and a pheromone trail was laid to it. Ants followed the brush as the trail was put down on the hard pebbly soil; and, as before, there was no organization into raiding formation but simply excited individuals running along the trail. There were perhaps 25 ants on the trail when the first one reached the box, entered, found a pupa, and started home. Almost immediately 3 others entered and found pupae. Their arrival back at the home nest caused a great outpouring of ants, and soon there were about 100 in the box and as many more on the trail. All of the pupae and larvae were hunted out and removed. When many ants returned without booty, the line of outgoing ants began to thin. The whole raid lasted 25 minutes — 4 minutes to the taking of the first pupae, 16 for removing all of the brood, and 5 more of hunting before giving up.

Immediately after the induced raid the ants started out on one of their own. Two hundred and seventy-two ants took part in this raid, so the colony probably had most of its forces involved in the induced one.

The difference between the induced raid and a natural one lay in the fact that the laid pheromone trail caused excitement and raiding action in individuals, while in a regular raid there was mass action, with a large group of ants leaving the nest together and staying in a compact group as they traveled along.

CONDITIONS UNDER WHICH RAIDS OCCURRED

Polyergus raids on the Reserve took place in the late afternoon but varied in time from colony to colony. The 0-26 colony raided early; its mean time for starting a raid was 4:21 PM EST (20 raids), while the Lawn Nest's mean was 5:36 PM (21 raids). Individual raids at 3 other colonies began at 4:50 PM, 5:08 PM and

6:55 PM. Four morning raids were seen at the Lawn Nest in 1959, but this seemed unusual and no others have been observed. Within a colony, raid time also varied widely: from 3:06 PM to 5:16 PM for 0-26 and from 3:50 PM to 6:25 PM for the Lawn Colony. Second raids could start as late as 6:45 PM for 0-26 and 7:30 PM for the Lawn Colony. The latest ended at 8:14 PM.

Colonies in fully exposed places where the sun was bright and the temperature high for longer time started their raids late. The 0-26 raids were early because nearby trees began shading the nest while the sun was still high in the sky, thus reducing the temperature to that tolerated by the ants. Single individuals could run rapidly into the shade of nearby dense grass at almost any time of day, but the raiding group could not form until they could circle on the soil surrounding the nest entrance. The upper limit of tolerance for *Polyergus* was about 91°F for air temperature 10 inches above the surface and 98°F on the surface. (*F. p. nitidiventris* workers could forage normally at these temperatures.)

Frequently during the morning or midafternoon an ant or two would stand at the entrance or move off to explore in the grasses. Then, in late afternoon, as the sun slanted low, or the nest was shaded so that both light and temperature dropped, ants began to come out one or 2 at a time. Sometimes the number increased gradually to full quota, but usually there would be a sudden outpouring which seemed to be in response to an incoming scout. Thus, the starting time of a raid was influenced by time and temperature and perhaps reduced light but seemed more directly dependent on the return of an ant which had laid an odor trail. This seemed quite clear for the late raid which began at 5:16 PM. The ants had begun coming out at 4:10 PM when temperature was reduced to 91°F.* From then on 20 to 50 kept exploring the edges of the nest but seemingly could find no direction to start out. Then suddenly at 5:08 PM more ants poured out, covered the nest, and explored into the grasses until they had organized a raiding party which left at 5:16 PM. It had seemed that weather conditions had been right, and the ants had been ready to start for about an hour before an odor trail was found.

Even at favorable temperatures the ants did not raid until midafternoon. The earliest raid seen began at 3:06 PM at 81°F (83°F on the ground). At 2:30 PM, when the watch began, there were

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*Temperatures are those 10 inches above the nest soil unless otherwise stated.

3 to 5 ants out; and the number increased to about 25 by 2:55 PM. At 3:04 PM many pushed out and started off 2 minutes later.

Polyergus raids did not take place at low temperatures. First raids of colony 0-26 never started at temperatures lower than 74°F and ended at 68°F or above. One second raid began at 71°F and ended at 69°F. The record for low temperature raiding was reached by a colony on another part of the Reserve, which started a second raid at 67°F and ended it at 65°F.

Ordinarily the ants raided under a great variety of light intensities ranging from 6,300 to 1,400 foot-candles over the nest at the beginning of a raid to from 2,600 to 700 foot-candles at the end. (In early afternoon, light readings might record as high as 10,000 ft-c.) One late third raid started at 400 foot-candles. Another colony began a record raid one cloudy evening when the light meter recorded only 216 ft-c, and the last ants returned in the semi-darkness of 46 ft-c.

Once a sudden drop in light preceding a storm seemed to prevent a raid. Approximately 50 ants were milling about on the nest at 4:10 PM when a solid black cloud reduced light from 1,500 to 800 foot-candles in 9 minutes, causing the retreat of all but 5 ants. (Temperature stayed high, dropping from 81°F to 79°F.) It continued dark, and rain began at 5 PM.

An approaching rain did not always discourage raiding. One group was caught in a downpour when about one-third was still on its way home.

In 1965, on 19 of the 31 days when no raids occurred, it rained in the afternoon or the ground was wet from a morning rain. On 11 days raids seemed to be prevented by low temperatures, and on one by drop in light. On one day in 1965, when weather conditions seemed ideal, the ants never came out in full force and made no attempt to form a raiding column. Once in 1964, again under seemingly ideal conditions, the ants ran about in full force for 30 minutes and a column moved out for 2 feet before all retreated. It seemed as if there were no trail to follow.

LENGTH OF THE RAIDING SEASON

Observations in 1964 did not begin until June 23, after raiding had started; therefore, in order to determine the beginning of the raiding season in 1965, the 0-26 nest was watched each afternoon, beginning on June 9. This day, as well as the 10th, 11th, and the 12th, was an adequate raiding day as far as weather was concerned; but only occasionally did a *Polyergus* worker come to the surface, loiter for a few seconds and then retreat. June 13 through June 17 were cool enough so that raiding would not have taken place in any season. On June 18 the *Polyergus* showed their first preliminary activity. They kept coming to the surface, one to 5 at a time. Some retreated quickly, while others moved away from the entrance to circle about on the bare nest area. At least 3 ants moved away into the grasses, exploring back and forth. This was interpreted as the first tentative scouting of the season. Next day, June 19, the first raid occurred. On that day workers began coming out of the nest at 3:55 PM, when the first flickering shade reduced the temperature from 90°F to 84°F. As a few circled about, some went off individually in different directions, moving rapidly out into the grass. At 4:45 PM an ant came in from the northwest and went directly into the nest entrance. Within 2 or 3 seconds *Polyergus* workers began pouring out, covering the nest area with a moving crowd which, 5 minutes later, began traveling off to the northwest on the initial raid of the year.

The raiding season probably started late in 1965, since June had been cold. The earliest raid ever seen was on June 11, 1959. Raiding seems to begin at the time when *F. p. nitidiventris* are accumulating their first pupae. A few newly formed pupae have been collected as early as June 5, in 1963 but were not found in 1965 until June 14.

Polyergus lucidus matures its brood more slowly. A colony dug into on June 15, 1965, had larvae but no pupae; and the earliest record of pupae was June 22, 1964. It would seem that raiding begins when *F. p. nitidiventris* pupae are just becoming available and while most *Polyergus* larvae are still small to medium size. Once raids have begun, they continue on almost very afternoon that the weather permits. The urge to raid seems especially strong during the early part of the season, reaching a peak in early July when there are the most double raids, when ants travel the greatest distance to outlying nests, when more brood is brought in, and when more *Polyergus* workers participate in the raids. By mid-August there is a dwindling of the number of ants which go on a raid. By this time perhaps all of the *F. p. nitidiventris* in the neighborhood have been raided once, twice, or more times; and the number of available pupae and larvae is dwindling. By early September the raiding season is about over. *F. p. nitidiventris* do not overwinter as larvae, and by the last of August no more are present. Pupae have been found in their colonies as late as September 19, but only a few were left at this time; and in colonies raided by *Polyergus* they had probably all emerged or been captured earlier. In 1964, the last 3 raids seen (August 27, 29, and September 3) yielded only 60, 47, and 37 pupae (no larvae); and there were only 82, 62, and 47 ants participating. It looked as if the raiding season would end soon after observations stopped on September 4. In 1965, on the last raid seen (September 3), 63 ants brought back only one pupa. Observations ceased on September 7.

NUMBER OF RAIDS MADE IN A SEASON

If, as we suppose, the raiding season begins about the middle of June, when pupae are accumulating, and lasts through the first or second week of September, by which time larvae will be gone and pupae are becoming scarce, then the raiding season consists of about 85 days. During 1964, the colony was observed on 50 days, during which time there were 29 raids on 24 days. Twenty-three of the raids were successful, while on 6 no brood was found. On this basis there may have been approximately 49 raids during the season — 39 of them successful and 10 unsuccessful. In 1965, during 54 days of observation, there were 34 raids on 22 days. Twenty-nine were fruitful and 5 were not. In an 85-day season the ants may have made 54 raids — 46 successful and 8 unsuccessful.

In the 2 seasons there were multiple raids on 30% of the raid days observed — 11 days of double raids and 3 of triple ones.

LOCATION OF COLONIES RAIDED

The *Polyergus* colony at 0-26 nested in a little hollow in a field which sloped down to a marsh at the southeast and up to woods on the north and west. There were *F. p. nitidiventris* colonies in all directions, but they were not randomly distributed. *F. p. nitidiventris* avoided nesting in woods or marsh, in heavy grass cover, in low spots on the field, and in a barren spot where gravel had been dug. Favorable places were on the grassy upland slope among sparsely scattered oaks (8 colonies), along a jeep road which made an open strip between marsh and woods (7 colonies), and in the lower field wherever vegetation was not too dense (4 colonies). The *Polyergus* raiding territory had a very irregular boundary which extended for 286 feet to the north and 114 feet to the northwest across fields, 218 feet to the west along the jeep road, 58 feet south toward the marsh, and 65 feet east to the gravel dig.

Measurements were taken of the distance travelel on 54 raids. The mean distance was 75 feet. On their longest raid the ants traveled over a little hill, across a valley, and up another hill to arrive exactly at a colony 286 feet away. The nearest colony nested only 15 feet from the *Polyergus* nest. During June the ants tended to raid nearby colonies; 20 raids averaged 56 feet per raid with a range of from 15 to 128 feet. By July they had to go farther afield to find new colonies. Eighteen raids averaged 103 feet and ranged from 18 to 286 feet. In August some raids were to distant colonies, and some were reraids of those nearby. Fourteen raids averaged 72 feet, ranging from 17 to 213 feet. The 2 September raids were short — 27 and 43 feet.

NUMBER OF COLONIES RAIDED

During both 1964 and 1965 a numbered stake was placed at each raided colony. In 1964, 17 different colonies were raided in the 23 successful raids seen. In 1965, in the 29 successful raids observed, 20 different colonies were visited. In 1965, the ants found only 2 colonies where they had been the year before; but they located 5 others 3 to 9 feet from a 1964 stake. This would seem to indicate an unusual amount of moving on the part of *F. p. nitidiventris* colonies, a behavior pattern which was probably instigated by the raids. This moving perhaps accounts for the fact that some unsuccessful raids were to what seemed to be obvious nest sites which had been recently deserted.

Reraiding of colonies was common practice. One colony only 24 feet away was known to have been raided on July 22, August 26, and September 3 of 1964 and again on June 20 (2 raids) and June 25 of 1965. During 1964, one colony was known to have been raided 4 times, one 3 times, and one twice. During 1965, 5 colonies were robbed twice and one 3 times. It would seem that, within a raiding season, most of the colonies would be visited more than once. The total number of colonies available may not have been more than about 25. This multiple raiding probably kept the colonies so depleted that they could not gather numbers enough to produce winged forms. Since *Polyergus* colonies tend to stay in one place for a number of years, they probably do not completely destroy *F. p. nitidiventris* colonies; but they may gradually diminish them to the extent that the *Polergus* colony cannot make a living and must move.

RAIDS WHICH ENDED IN FAILURE

Occasionally a raiding group, typical in all respects, failed to find a colony. This seemed to be the result of misinformation on the part of a scout, because the raiding forces were as large as usual and the spots they stopped at were just as definite. The usual routine was followed at trail's end: that of a compact mass of ants digging in around pebbles, leaves, and grass. When no nest was found, the group began moving in widening circles, out as much as 3 feet. After 2 to 7 minutes of futile search some ants turned homeward, while others dug for another 10 to 20 minutes before giving up. Some of the wrong spots seemed quite evidently places where ants had been living. One had a pile of excavated soil before a wide open entrance into which the ants plunged. Once a colony which had been raided 3 times previously erected such a good barricade that the *Polyergus* never did get in, although they did not give up for 22 minutes. (Later I dug the nest and found the colony still there.) During the 2 years 11 failures occurred in 63 observed raids. Thus, 17.6% of the raids ended in failures which seemed to be due to misinformation. One ended in disaster because the terrain was too severe. The ants started up an almost perpendicular bare bank, but many lost their footing and could not get to the top. The whole group became disorganized, and eventually all returned home without going any farther.

SPEED OF TRAVEL AND TIME REQUIRED FOR A RAID

The time of an entire raid was considered as the interval between the starting out of a raiding column and the return of the last ant. This varied greatly, depending on distance traveled, time required to get into a nest, amount of brood to be brought out, and the length of time that some ants delayed at the nest before starting home. For 51 raids the mean time was approximately an hour (63 minutes). The extremes were 20 minutes for a raid on a colony 15 feet away, to 2 hours and 19 minutes for one on the most distant colony 286 feet away. June raids took a shorter time, averaging 47 minutes in contrast to 73 minutes for both July and August and indicating again that near colonies were raided first.

The preraid organizing, when many ants were moving about on the nest, took from 2 to 25 minutes and averaged 9.6 minutes. The time taken to reach a raided nest averaged 23 minutes and varied from 5 to 65 minutes. The opening of a nest, its penetration, and the emergence of the first ants with loot averaged 4.4 minutes. If the entrance was not obstructed, they could enter immediately; if it was barricaded or guarded, they might require as much as 13 minutes to free it. Once the ants entered, they would have the first brood out within a minute or two. The journey back took a shorter time than the outward one had required. The mean time required for the first ant to reach home was 15.9 minutes with a variation of 3 to 47 minutes. The last ant reached home anywhere from 3 to 40 minutes later, the mean being 17 minutes.

The outgoing group of raiding ants moved at a fast pace, in spite of the fact that individuals were constantly running backward and to the side as well as forward. The mean speed of travel to raided nests was 3.1 feet a minute, and the extremes varied from 1.1 foot to 4.9 feet. The ants speeded up when they crossed bare spots at very high temperatures, but the terrain also influenced speed. Travel uphill or through rough areas with large grass clumps slowed speed; and sometimes, in places with leaf cover, the group spread out a bit and explored under leaves as they moved along. It was not surprising that individual ants made better time returning to the home nest, even when burdened with brood. The mean speed was 4.7 feet a minute, with individual records varying from 2 to 6.5 feet.

NUMBER OF ANTS TAKING PART IN A RAID

For 47 raids ants were counted as they returned to the home nest. Not all of the *Polyergus* workers went on each raid, and the number varied considerably from day to day. However, in both years the force reached a peak in early July and dwindled in August. In 1964, the largest number seen on a raid was 370 (on July 10); and in 1965, it was 536 (on July 3). The smallest were 47 (Sept. 3, 1964) and 63 (Sept. 3, 1965). Nineteen raids counted in 1964 gave a mean raiding force of 231, while 28 raids in 1965 averaged 307 workers. It would seem that 0-26 is a vigorous and growing colony, perhaps one of the largest on the Reserve. Counts at other colonies (made for comparison in June and July of several years) gave raiding groups consisting of 272, 258, 194, 112, 54, 31, and 13 ants.

AMOUNT OF BROOD COLLECTED

The success of a raid was unpredictable and until late summer bore no correlation to the number of ants participating in it. One raiding party of 313 ants brought in only 8 pupae and 5 larvae, while another of 310 ants returned with 184 pupae and 32 larvae. The most successful raid took place on July 10, 1965, when 505 ants brought back 446 pupae and 34 larvae. The colony had not been raided before that season.

A raid did not necessarily wipe out the brood in a *F. p. nitidiventris* colony. On June 20 a group of 338 raiding ants secured 235 pupae and 78 larvae. Fifteen minutes after all were back in the home nest they organized another raid, with 284 ants, to the same colony and took 73 pupae and 19 larvae.

Brood collected in 19 raids in 1964 averaged 120 (98 pupae and 22 larvae) a raid. If an estimated 40 successful raids took place during the season, the *Polyergus* captured approximately 4,800 young ants (3,920 pupae and 880 larvae). Since there were probably not more than one-and-a-half times that number of adult *Formica* in the mixed colony, and since many workers live for a number of years, it would seem that a fair proportion of the brood brought in is used for food. The success of the 1965 season was similar. Twenty-eight raids brought in a mean of 116 young ants consisting of a mean of 90 pupae and 26 larvae.

Ants counted as they reached the home nest fell into three categories: those with pupae, those with larvae, and those with nothing. The proportion varied greatly from an extreme of a successful raid in which 438 carried brood and only 18 did not, to an unsuccessful one in which 32 carried brood and 410 returned without. In 1964, 48% of the ants returned wihout brood, while in 1965 the unsuccessful ones constituted 66%. The second season may have been simply a bad year; or perhaps after a *Polyergus* colony reaches a certain size, the number of brood captured depends not on the strength of the raiding force but upon the number of *F. p. nitidiventris* larvae and pupae available.

An unusual method of collecting brood was seen in 1967 when a *Polyergus* colony raided another *Polyergus-Formica p. nitidiventris* colony at least twice. On the raid seen on August 15, the timing was perfect. Ants from nest "a" traveled for 28 minutes to nest "b," reaching it 8 minutes after all of its *Polyergus* had started on a raid. There was no barricade, and no fighting, and the 76 ants from nest "a" made off with 68 pupae and two larvae. The last ant, carrying a pupa, left just as the nest "b" *Polyergus* returned. They had also made a successful raid, in which 98 ants returned with 97 pupae (and many ants started off immediately over the same trail to bring in more pupae).

Nest "a" had been discovered in 1966, and it seems possible that it is the old Lawn Colony which remained in one place from 1956 to 1965. If this is true, it had moved 61 feet late in 1965 or early in 1966.

RELATIONSHIP WITH OTHER ANTS

The 0-26 colony raided only *F. p. nitidiventris.* The Lawn Colony raided *F. p. nitidiventris, F. lasioides* Emery, and *F. neogagates* Emery; but only the first species were seen at the home nest.

Once, by mistake, members of the 0-26 colony entered a nest of *F. fusca* Linne. They were engaged in a fight and succeeded in taking away only 4 pupae.

Ordinarily a column of *Polyergus* did not disturb other ants which they passed by; but when some individuals aroused a *F. subintegra-F. fusca* colony by investigating openings in the nest, they were attacked by both species of the mixed colony and some were killed. Once *F. obscuriventris* Forel workers intercepted *Polyergus* individuals returning home with brood and hijacked a few pupae.

SUMMARY

At the Edwin S. George Reserve, in southern Michigan, slave-making raids of the ant *Polyergus lucidus* Mayr took place in the late afternoon (3:06-7:30 PM), at high to medium temperatures (91°-67°F) and reduced light (6,300-216 foot-candles). The slave ants were *Formica pallidefulva nitidiventris* Emery, but *F. neogagates* Emery and *F. lasioides* Emery were also raided by some colonies.

It was concluded that scouts individually find nests and lay odor trails back to the home colony. Raiding groups go directly to the nests to be plundered. Pheromone trails, which ants would follow, could be made from a solution of *Polyergus* workers crushed in dichloromethane. A raid on a *F. p. nitidiventris* colony, in a box placed 6 feet away, was induced in this manner.

The raiding season began in mid-June and lasted into September. It coincided with the time when the slave species had pupae in the nest. It was estimated that about 50 raids could be made in an 85-day season. On some days double, or even triple, raids occurred.

Distances traveled to a raided colony ranged from 15 to 286 feet. Ants in a raiding group traveled about 3 feet a minute. An entire raid might be finished in 20 minutes or might take as long as 2 hours and 19 minutes. The mean time was one hour.

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A NEW *OMOPHRON* AND A NEW *SIAGONA* FROM THE PHILIPPINES (COLEOPTERA: CARABIDAE)*

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The following two new species from the Philippines constitute zoogeographically important range extensions of the carabid genera *Omophron* and *Siagona.* They are described now so that I can refer to them in discussion of the distribution of Carabidae in the Indo-Australian Archipelago in Part IV of my "Carabid Beetles of New Guinea."

Tribe OMOPHRONINI

Genus *Omophron* Latreille

Omophron is usually considered to be the only genus of its tribe. The insects are broadly oval, multistriate, often complexly marked carabids which inhabit sandy shores of rivers and lakes. They are usually nocturnal and stay hidden in closed burrows in the sand by day, but they may be routed out by water thrown over the sand in which they are hiding.

Distribution of the genus. Africa and Madagascar, Europe and Asia to Japan, and North and northern Central America; but not South America and not the Australian Region. An old record for New Caledonia is considered an error (Banninger 1918, p. 109). In the Oriental Region, species are numerous from India to northern Indo-China, and a few occur south through the Indo-Chinese Peninsula, but none is known from the Malay Peninsula and, until now, none has been found in the Indo-Australian Archipelago or the Philippines, so the present new species from Luzon considerably extends the known range of the genus.

Omophron luzonicus sp. nov. (Figs. 1, 2)

Types. Holotype ♂ (Museum of Comparative Zoology, Type No. 27,931) and 20 paratypes all from Central Plains of Luzon, Philippine Islands, Feb. — Sept. 1945, collected by myself. The entire type series was taken from sandy river banks and bars, chiefly along the Rio Pampanga.

Description. Form and pattern as figured; back of head and discal areas of pronotum and elytra blackish green, with marginal pattern

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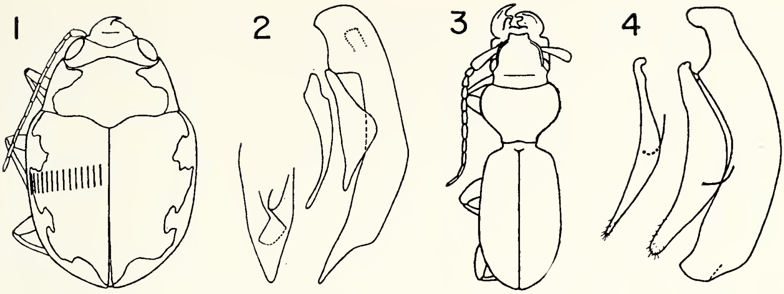

Figures 1 and 2. *Omophron luzonicus,* n.sp. Figures 3 and 4. *Siagona sinistra* n.sp.

whitish testaceous; below testaceous with a broad median brown area from prosternum to 2nd ventral segment; appendages whitish testaceous; most of upper surface including elytral intervals with lightly impressed but distinct isodiametric microsculpture. *Head:* mandibles with upper edge of scrobe only moderately raised; antennae with segment 1 with 1 seta, segments 3 and 4 with usual subapical setae but without extra setae on outer margins; clypeus bisetose, slightly or indistinctly margined, with suture rounded or subangulate; surface of head at sides and posteriorly moderately punctate, front nearly impunctate; subocular ridges present, space between ridge and eye rugose-punctate. *Prothorax* with pronotal disk slightly depressed basally, rather finely and sparsely punctate, a little more closely so anteriorly; lateral marginal channels rather narrow, not punctate; median line lightly impressed, slightly abbreviated at both ends. *Elytra* convex as usual; each with 15 moderately impressed, lightly punctate striae; striation almost entire except striae 2-3 and 7-8 ending about 1/3 from apex (varying in exact length and connections); stria 11 reaching to or within apical 1/4; intervals moderately convex, impunctate, but with microsculpture as described. *Below:* sterna and first 2 ventral segments with scattered punctures of moderate size; epipleurae not punctate; suture between prosternal and proepisternal processes (behind anterior coxae) usually not impressed; middle coxa with 1 seta, on inner side. *Male* with 2 basal segments each front tarsus and first segment middle tarsus slightly dilated, with sexual pubescence below; copulatory organs as figured (Fig. 2). Length 6.0-6.5 mm.

Remarks. I am unable to say from which Asiatic stock this species is derived, for its characters are mixed. In Banninger's (1918) grouping of the species of *Omophron*, it falls in the first half of couplet 11, with *axillaris* Chaudoir and certain African species. In Andrewes' (1929, pp. 141-143) key to the *Omophron* of India, Burma, etc. it falls between *axillaris* and *rotundatus* Chaudoir, but differs from both in possessing distinct subocular ridges. It differs further from *axillaris* in having a longer 11th elytral stria, less coarsely punctate head and pronotum, and more obvious microsculpture on elytral intervals, and from *rotundatus* in greater extent of the dark color pattern and in finer punctation of head and pronotum. The wide extent of the dark color and the fineness of the punctation distinguish it also from *saigonensis* Chaudoir. It is superficially similar to *stictus* Andrewes (1933) of Tonkin, but *stictus* has a strongly margined clypeus and is relatively coarsely punctate above. The Museum of Comparative Zoology possesses, and I have examined, specimens of all of these species except *saigonensis*, which I know only from descriptions.

Tribe SIAGONINI

Genus *Siagona* Latreille

This is the principal or only genus of its tribe — whether *Luperca* of Africa and India and *Enceladus* of South America should be included in the same tribe is still an open question. The species of *Siagona* are characteristically shaped, flattened insects which are said to live sometimes under stones, sometimes under bark or between leaf-sheaths of plants.

Distribution of the genus. Africa and Madagascar, southern Europe, Asia Minor etc., and the Oriental Region. In the latter, species are numerous from India to Indo-China, and at least two occur southward into the Malay Peninsula, but only one, *insulana* Andrewes (1936) of Java, has been recorded from the islands east of Asia. The present new species from Mindoro considerably extends the known range of the genus.

Siagona sinistra sp. nov. (Figs. 3, 4)

Types. Holotype ♂ (California Academy of Sciences) and 2 paratypes (♂ in Museum of Comparative Zoology, Type No. 31,603; ♀ in California Academy of Sciences) all from San José, Mindoro, Philippine Islands, Oct. 1945 (E. S. Ross). The specimens were "found in rotting bark of living Buri palm (ESR)."

Description. Form as figured; black, appendages piceous; above rather shining, unevenly and rather sparsely punctate and pubescent, mostly without distinct microsculpture; labrum, sides of neck, impressions of pronotum, margins and apices of elytra, and much of lower surface with more or less distinct, close, nearly isodiametric microsculpture. *Head* large; clypeal suture impressed; lateral ridges rather thick, becoming obsolete posteriorly above or just back of posterior edges of eyes, rounded anteriorly, not distinctly interrupted at the bend but obliquely grooved externally; neck constriction impressed; surface of head unevenly punctate, almost impunctate on middle of front and behind neck constriction; antennae with first segment moderately, not suddenly clavate; supra-maxillary plates dilated laterally, angulately rounded; mandibles of both sexes expanded and margined externally near base, those of male broadly, irregularly impressed and wrinkled above near base, the left one with a strong tubercle on inner side of upper surface. *Prothorax:* pronotum with fine median line and deeper, uninterrupted lateral sulci; surface of pronotum punctate across base and apex and near lateral margins, and much more sparsely so on disk. *Elytra* each with a distinct, short plica above the humerus, directed backward and outward; elytral surface rather finely punctate, the punctures sparse on the disk. *Inner wings* fully developed. *Stridulating files,* under lateral margins of prothorax, present in both sexes. *Male* with mandibles modified as described above; copulatory organs as figured (Fig. 4). Length: 19-19.5 mm.

Remarks. Twenty-seven previously described species of *Siagona* are recognized from the Oriental Region. Most of them are included in Andrewes' (1929, pp. 178-181), "British India" key, and 18 of them are represented in the Museum of Comparative Zoology, although not all by males. Nevertheless I have had difficulty in placing the present new species satisfactorily.

The most striking characteristic of the new species is the tubercle of the left mandible of the male. Carinae or tubercles are variously developed on the upper surface of the mandibles inwardly near the base, in males only, in different Oriental *Siagona.* Many of the species lack them. The males of *obscuripes* Chaudoir, *strata* Dejean, and *baconi* Chaudoir have a longitudinal carina about equally developed on each mandible, the carinae being respectively weak, moderate, and strong in the three species named. The male of *induta* Chaudoir is said to have an elevated boss on each mandible, that on the left higher than that on the right. The male of *crassidens* Bates is said to have only the left mandible tuberculate. The males of *angulifrons* Bates and *rustica* Andrewes are said to have the *right* mandible carinate, the left one only vaguely or not so. Andrewes

(1929) describes the condition in some other species. Of previously known Oriental *Siagona,* only *crassidens* (of southern Indo-China) has the male mandible armed nearly like that of the present new species, but the latter, compared with Bates' (1889) description of *crassidens,* is larger, with head ridges more abbreviated posteriorly, with sparser elytral punctation, and with the mandibular tubercle not bilobed.

Andrewes' key (referred to above) is based chiefly on asexual characters and does little to help place the new species. The latter does not fit into the key: it is winged and large (couplets 1 and 2), but the lateral ridges of the head do not nearly reach the neck construction. In wings, size, and head ridges the new species is like *sublaevis* Chaudoir, which is known only from southern Indo-China, Siam, and the Malay Peninsula, and which is therefore omitted from the "British India" key. There are two specimens, both females, of *sublaevis* in the Museum of Comparative Zoology, and the female of the new species matches them in most characters including the presence of an unusually distinct, short, post-humeral plica on each elytron. The only significant difference I note is sparser punctation of the disk of the elytra in the new species. But Chaudoir (1876) described *sublaevis,* from Bangkok, from a good series of both sexes, and the male has no mandibular tubercle. The Javan *insulana* Andrewes (1936), of which I have one male, is a smaller species, without distinct post-humeral elytral plicas, but with nearly similar head ridges. It lacks mandibular tubercles.

Taking one consideration with another, I think that the new Philippine species most likely represents the stock of *sublaevis,* and that the mandibular tubercle of the male has been developed independently, not inherited from an Asiatic ancestor, and I suspect that *insulana* may prove to be a modification of the same stock rather than a relative of *fabricii* Andrewes as Andrewes (1936) originally supposed. It will require a revision of a number of Oriental *Siagona* to decide these possibilities.

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PREDATORY AND SEXUAL BEHAVIOR OF THE SPIDER *SICARIUS* (ARANEAE: SICARIIDAE)*

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For a period of over 20 years, from 1911 to 1933 (Bonnet, 1945), Gerhardt published observations on the sexual behavior of spiders, describing sperm induction, charging the pedipalps with sperm, as well as mating. The observations (Gerhardt, 1924, 1927, 1930, 1933) concerned representatives of all available families with the hope of obtaining comparative data. Different groups of spiders have different methods of sperm induction and different mating positions. Gerhardt was more interested in the mechanical aspects of mating than in courtship behavior. A helpful summary (in English) of the observations of Gerhardt, Bristowe and others is provided by Kaston (1948). Only in the last few years have there been some experimental studies, including observations on the copulatory behavior of spiders after removal of their palpi (Rovner, 1966, 1967). Surprisingly, courtship continued normally although both pedipalps had been amputated in the penultimate instar and neither sperm induction nor copulation was possible.

During sperm induction, the spider makes a web with silk from the posterior spinnerets. A small area in the web, a substrate, is prepared with silk from spinning glands in the epigastric area (Melchers, 1963; Marples, 1967). On this substrate a drop of sperm is deposited. The sperm is drawn into a duct within the pedipalp of the spider, perhaps by resorption of a fluid previously secreted by the surrounding glands (Cooke, 1966). In some haplogyne spiders (which lack an epigynum, a plate with copulatory pores separate from gonopores), both pedipalps are inserted into the drop simultaneously; in Orthognatha (the "tarantulas" of American parlance) and most other spiders, alternately. Some spiders attach the drop below the web and stand above while charging the pedipalps; others deposit the drop on the upper surface and reach around the edge to charge the pedipalps through the web. The pedipalps are recharged after mating.

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There is an enormous literature on courtship, partially summarized by Kaestner (1965, and in press). The possible mating positions are summarized by Kaston (1948). In the Orthognatha and many haplogynes, the male stands with his body at an angle to that of the female, or with his dorsum applied to her venter, the partners facing opposite directions. In others, mainly hunting spiders, the male mounts the back of the female, facing in the opposite direction. In many web spiders he crawls under the female, venter to venter, facing the same direction. In others the male and female position themselves venter to venter facing opposite directions. In some, the female lies on her side with the male over her. In most haplogynes both pedipalps are inserted at the same time; in other than haplogynes only one is used or, more commonly, the pedipalps are alternated.

Dabelow, in a recent paper (1958), described differences in mating position of different "races" of the haplogyne *Scytodes thoracica* from the Mediterranean, Dalmatia and central Europe. The female has sclerotized grooves on the venter of the abdomen which receive the jaws of the male during copulation. Females of the Mediterranean race took a vertical position with the male horizontal. In the central European race both tended to assume a vertical position facing the same direction. In the Dalmatian race the male crawled under the female and mated venter to venter. As no taxonomic revision of European *Scytodes* exists, it is difficult to interpret the results. The variation in mating position might reflect geographical variation or the "races" may actually represent separate species. Whatever the factors, apparently this behavior is not as conservative as formerly thought. A *Scytodes* sp. from Arizona was observed by W. Eberhard (unpublished) to take still another position. Its chelicerae did not bite into the sclerotized abdominal grooves at all during mating.

One family not represented in any of these studies and never heretofore recorded is the Sicariidae, a small family of spiders mainly of the southern hemisphere, Africa and South America. Sicariids, as an adaptation to their mainly arid and hot desert habitat, bury themselves in sand (Reiskind, 1966) and sand grains from their surroundings adhere to their setae, giving the spiders the color of their background. *Scytodes* is often erroneously placed by European arachnologists in the haplogyne family Sicariidae. Most European arachnologists are completely unaware of the nature of *Sicarius,* having seen only preserved specimens. Judging by the observations to follow, the families Scytodidae and Sicariidae, while related, are nevertheless distinct.

A taxonomic revision of the family Sicariidae has never been made. Such a study would be time consuming and difficult — the holotypes of the numerous names would have to be consulted in various South American museums. The species in our cultures are thus labelled no. 1 (from Tucumán Province, Argentina) and no. 2 (from Lima, Peru). Voucher specimens have been placed in the Museum of Comparative Zoology. The life history observations recorded here come from culture no. 1.

FEEDING

Sicarius is a powerful spider that feeds on passing insects, rapidly emerging from the sand when disturbed. The prey is not chewed but, like the prey of many spiders, apparently liquified inside its integument and then sucked out. No use at all is made of silk in prey capture. Small prey (e.g. house flies, mealworms) are taken along when the spider digs itself into the sand, and are never left and picked up later. However, a grasshopper 1 1/2 times as long as *Sicarius* was bitten and left, to be attacked again shortly afterwards. When the prey was somewhat subdued the spider began feeding, changing the place of biting and turning the prey during the next five hours. The prey was then left during the evening, and the spider buried itself; the next morning, the spider emerged and went straight to the grasshopper shell about 5 cm away, bit into it and fed for a while. Whether it fed during the night is not known. (It is doubtful that sicariid eyes produce a picture image.)

MATING

Of the contents of one egg case raised, four specimens matured: one female and three males. After two males matured in June 1967, they were "restless" and often were seen against the walls of their plastic container, rarely buried. On the 20th of July, 1967, one male was placed with a female, one with an immature male thought to be an adult female. They buried themselves after the disturbance. The male placed with the juvenile specimen showed no interest in it. The juvenile molted on 21 October 1967, and turned out to be a male.

The other male, however, surfaced after about two hours and walked about. Suddenly he stopped and began to dig with the front legs, thus exposing the posterior end of the abdomen of the female, who was facing the opposite direction. After the female was dug out or in part emerged from the sand (at about 15:30), the male and female stood face to face, the fronts of their carapaces touching. The male gently felt the dorsal abdomen of the female with his long legs.

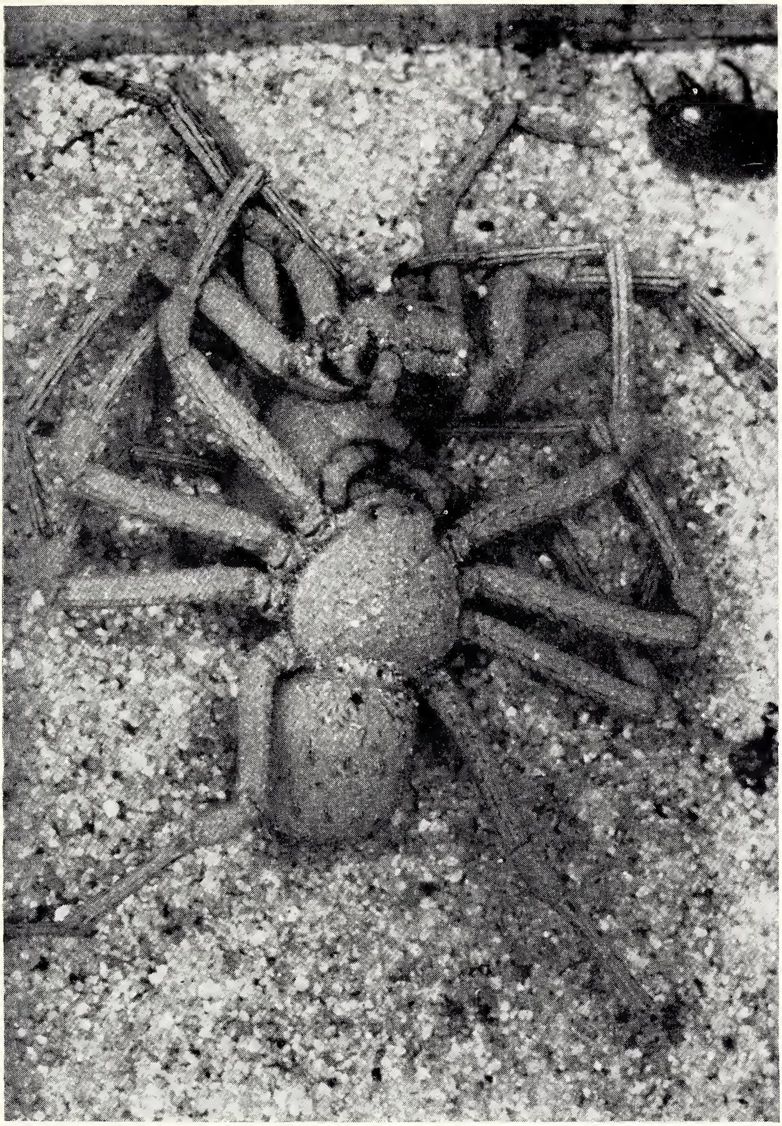

Fig. 1. *Sicarius* sp. mating; each individual is about 18 mm in body length.

Then with a sudden movement the male turned the female into mating position, clamping her down with his legs (Fig. 1), and both pedipalps were inserted immediately (at 15:35). The pedipalps "wiggled" slightly. Once in a while the female made a slight motion (Fig. 1). After 18 minutes (15:53) the animals suddenly separated, the female moved about 7 cm to the side and rapidly dug herself in. The male stood for about 30 seconds, then moved off about 20 cm and buried himself.

On 17 Setpember 1967, at 20:00, the same male was placed with the same female again. He moved slowly about, but stopped when he touched the partly exposed abdomen of the female. Suddenly he pulled her out of the sand sideways; the female did not resist. The male went through the same motions described above. For a short time before turning the female on her back the front ends of the male's and female's carapaces touched. The spiders separated 30 minutes after starting copulation, moved in opposite directions, but did not bury themselves (perhaps due to relative darkness). Unfortunately no movie camera was available to record the sequence.

SPERM INDUCTION

The night following the first mating, neither of the mated spiders appeared active. Both remained buried. At 22:30 the following night (21 July 1967), I was surprised to find the male hanging in a web, for I had not seen any use of spinnerets or silk before. The web consisted of very coarse strands of unequal width, diagonally from the side to the lid of the container, attached below to a vertical cardboard partition, above by several threads to the screen lid. The threads, later examined under the microscope, consisted of at least 10 strands matted together into a ribbon, flat in places. The male was hanging head up (Fig. 2), and the alternate forward and back movements of his pedipalps suggested that this might be the sperm web. A minute later the spider slid down and both pedipalps touched a yellowish-white droplet at the junction of the silk threads (Fig. 3). Both pedipalps touched the droplet at the same time, but did not move at all. The lights were turned on without apparently disturbing the spider (previous observations had been made with a dim flashlight). An attempt to lift the lid (at 22:45), with the hope of photographing, however, disturbed the silk threads. The spider jumped down onto the sand and buried himself. The lack of threads with other males suggests that the web was destroyed and eaten after use.

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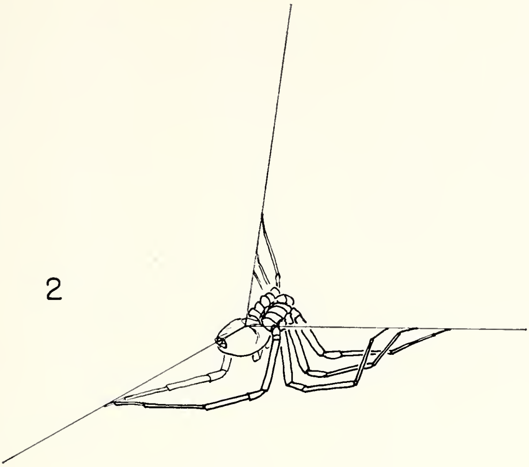

Fig. 2. Male depositing sperm on sperm web.

LIFE SPAN

From a newly hatched eggcase given to me by Dr. W. K. Weyrauch in February 1965 in Tucumán, we reared two males and one female that molted to maturity during June 1967 and one male that matured in October 1967. The individuals took more than two years to mature. Individuals of species 2 from Lima, Peru, were 1 1/2 years old and less than half grown in August 1967. An adult individual collected on 2 April 1965 (under a log in pasture near Santiago del Estero) appeared moribund in July, 1967; it had not fed for some time, no longer buried itself, and looked emaciated. After placing it in alcohol, I discovered it was a male. (Male sicariids differ from females by having longer legs and by modifications of the pedipalps that are not readily apparent). As far as we know, the individual had never molted, had lived at least two years beyond reaching maturity, and was probably at least four years old. After killing the male, we discovered that its container had become moldy, a condition that would be injurious to most spiders; thus it may have been moribund not from old age, but from poor laboratory conditions.

DISCUSSION

Although related, sicariids are very different from scytodid spiders. While the slow scytodids overpower their prey by spitting a viscid, entangling substance, the sicariids are strong, fast moving predators

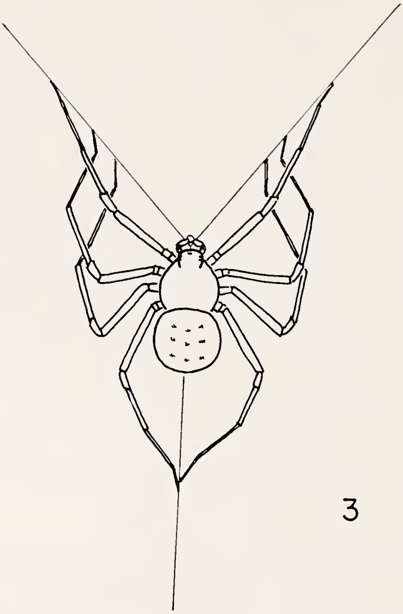

Fig. 3. Male taking up sperm into pedipalps.

that overpower their prey with force and poison. Both sicariids and loxoscelids lack the adaptations of scytodids for their unusual method of prey capture: the high-domed carapace containing the glands used for spitting, and the short, stout fangs with the aperture of the gland duct at their midpoint. (The Loxoscelidae are also at times placed in the Sicariidae, but probably with more reason than the Scytodidae.)

The sicariids courtship act of digging the female out of the sand is probably unique among spiders, but the mating position is similar to that of scytodids, a group in which there is some variation (see above). As in other haplogyne spiders (but unlike orthognath "tarantulas"), both pedipalps are inserted into the gonopore at the same time.

Another habit shared with other haplogyne spiders, but not with orthognath "tarantulas", is that both pedipalps are inserted simultaneously into the sperm drop during sperm induction. An exception is the haplogyne dysderid, *Harpactes rubicundus,* which uses the method exhibited by most spiders, continuously alternating the pedipalps for sperm filling. Members of the orb weaver genus *Tetragnatha* use the haplogyne method of sperm induction (Gerhardt, 1927), although the absence of an epigynum in *Tetragnatha* is believed secondary. *Filistata,* though it lacks an epigynum, is considered (there abides a controversy) to belong to a separate line of evolution because of the presence of a cribellum. The *Filistata* male alternates the pedipalps in mating and in sperm induction, as do the orthognaths (Gerhardt, 1930).

There is little literature on the significance of longevity of spiders. But it is striking that spiders with genitalia considered primitive are long lived, those with more typical genitalia are short lived. A short life span of one or two seasons and rapid succession of generations must be of selective advantage, as it is a charateristic of the most successful groups of spiders. Selective advantages might be larger numbers of progeny, increased number of generations, and ability to colonize new situations, especially areas with short seasons, etc. Table I summarizes the available data on longevity of spider species with simple genitalia.

Primitive groups of hypochilid spiders, however, are short lived. Adult *Hypochilus gertschi* disappear in the fall, adult females reappearing in July. Probably it takes two years to mature (W. Shear, in letter). During an autumn visit to Chile (March, 1965), only juveniles of *Thaida peculiaris* (=*Austrochilus manni*) were found, no adults.

Adult Orthoganatha (e.g. Theraphosidae) molt once or twice a year during most of their long lives, except during the last year or two. Haplogyne spiders do not molt after reaching maturity. In molting, presumably, spiders shed also the lining of the seminal receptacles and with it any stored sperm. Thus, it is rare for a captive theraphosid to produce an egg sac unless the animal is a recent captive. In contrast, some haplogyne females even after years of captivity may still produce fertile egg sacs from previous matings.

Another specialization of scytodids that separates the family from other groups should be pointed out. On the venter behind the gonopore the female has sclerotized grooves into which the fangs of the male are usually inserted to hold the female during mating; this structure is not present in sicariids or loxoscelids. Perhaps these grooves represent a preadaptation toward the evolution of an epigynum (the plate bearing separate copulatory pores which lies in front of the gonopores) present in most higher spiders.

	time to maturity	male life span beyond maturity	total life span of female	molt as adults
Theraphosidae	ca. 3 yr.	up to 1 yr.	to 20 yr.	♀♀ yes
Sicariidae[1]	2+ yr.	2+ yr.	4+ yr.	no
Loxoscelidae	1 yr.	1-2+ yr. *(laeta)*[3]	2 1/2 yr. *(reclusa)*[2] 4-6 yr. *(laeta)*[3]	no
Scytodidae[4]	1-1 1/2 yr.	max. 1 yr.	3 yr.	no
Diguetidae[5]	?	?	1+ yr. beyond maturity	no
Plectreuridae[1]	2-3 yr.	?	? 4+ yr.	no
Dysderidae[6]	1 1/2 yr.	at most 1 1/2 yr.	4-5 yr.	no
Most higher spiders and most cribellates	less than 1 yr.	usually die after mating	at most 1 season after maturity	no
cribellate Hypochilidae[7]	? 2 yr.	die after mating	2-3 months	no
cribellate Filistatidae[8]	? 1-2 yr.	die after mating	5-7 yr.	no

Table I. Length of life of spiders considered "primitive" on basis of their simple genitalia.

[1] personal observation

[2] Hite, 1966

[3] pers. comm. Mrs. F. Coyle, A. Spielman, R. E. Wheeler from colonies kept at Cambridge, Mass.

[4] Dabelow, 1958, on *Scytodes thoracica*

[5] pers. comm. W. Eberhard

[6] Cooke, 1965a, b, on *Dysdera crocata.*

[7] pers. comm. W. Shear

[8] Gerhardt, 1930; Lowrie, 1965

In the Pholcidae, this same structure, a swollen area held by the male with his chelicerae, is in front of the gonopores in place of the epigynum of other spiders. However, as indicated by this genital structure of the female and the unusual pedipalp structure of the male, Pholcidae are not closely related to other spiders. Further evidence for this comes from the method of sperm induction, quite different from that of any other spiders: the sperm drop is taken into the mouth aided by the third legs and from there to the palps. As in other haplogyne spiders, both pedipalps are inserted simultaneously into the female gonopore (Gerhardt, 1927).

A unique, as yet unmentioned, behavioral character of sicariids is the eggsac. Made of sand grains, it resembles a mud-dauber nest rather than a spider eggsac (Levi and Levi, 1968, p. 28). The method of construction is unknown. Scytodids carry their eggs in a loose sac; loxoscelids attach their eggs, wrapped in very few threads, in their webs, as do plectreurids. Dysderids keep their eggs at the inner end of the tube with no silk around the eggs (*Ariadna* and *Dysdera*). Diguetid eggs are contained in strong silk sacs within a strong silken tube.

SUMMARY

Sicarius feeds by overpowering passing insects. No use is made of silk in feeding; the prey seems to be slowed down by poison. The male begins courtship by digging the female out of the sand and stroking her. The mating position was observed (Fig. 1); both pedipalps were inserted simultaneously. A female will mate repeatedly. In recharging the pedipalps, both were dipped simultaneously into the sperm drop on a specially made web and held in the drop without visible movement. In their long life span sicariids resemble other haplogyne spiders (although there are some exceptions). In its behavior, *Sicarius* resembles *Loxosceles* more than *Scytodes*. Construction of the unusual eggsac of *Sicarius* has not been observed.

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A NEW *PHEIDOLE* WITH REVERSED PHRAGMOSIS (HYMENOPTERA: FORMICIDAE)*

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INTRODUCTION

A number of ants have plug-shaped heads, known or assumed to be used to stopper the nest entrance. This phenomenon, called *phragmosis,* is best understood in certain groups of *Camponotus* and Cephalotini (e.g. Wheeler 1910: 209-212, Szabó-Patay 1928, Creighton and Gregg 1954), but Wheeler (1901: 534; 1927) also described species with phragmotic-like heads in *Pheidole, Crematogaster* and the dacetine genus *Colobostruma,* while Patrizi (1948) published the problematical *Solenopsis (Crateropsis) elmenteitae* (placed by Ettershank, 1966, in *Oligomyrmex*). In most of these forms, either the queens or the soldiers, or both, are the phragmotic castes; in *Colobostruma leae,* the assumed phragmotics are the queen and the monomorphic workers.

In the new species of *Pheidole* described below, phragmotic behavior at some stage of the life cycle is indicated only for the queen caste, and even then is inferred from her aberrant body form. But in this case, the plug is formed, not by the head, but by the highly modified gaster (Figs. 6 and 7).

Two queens showing this plug-like modification of the gaster were taken separately from rotten wood in rain forest in the general vicinity of Manaus during my collecting trip of 1962 in the Brazilian Amazon. In one case, and possibly in both, the queens belonged to definite colonies with workers, soldiers and brood. (Notes on collection M-60 are ambiguous because two *Pheidole* queens, one of *embolopyx* and one of a totally different species, were in the vial with this number, but the notes state that "the" queen was taken apart from the soldiers, workers and brood. Probably one of the two queens was taken up in the aspirator along with bits of rotten wood without my knowing it.)

The queen's thickened scape base (with a gelatinous sheath) and the largely smooth and shining alitrunk with overhanging scutal margins, are "protective" characters suggesting social parasitism as a way of nest-founding for this caste. The strong similarities in color, sculpture and pilosity between the queens and the accompanying

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soldiers weigh against considering them as different species, so perhaps the queens of the new species found nests by entering the nest of some other *Pheidole* species. If so, then what is the need for the phragmotic posterior in the queen? Does she enter a circular burrow in a twig or in rotten wood in or near the host nest, and seal herself off from the host workers by phragmosis?

Whatever the truth proves to be, it will certainly make a fascinating story when the life history of the new *Pheidole* is better known. One interesting but inconspicuous feature is the presence of a few short, fine, outstanding setae ranged around the rim of the phragmotic face of the gaster (Fig. 6); undoubtedly these serve as "vibrissae", or sense hairs that inform the insect as to how snugly the plug is fitting into whatever passage or entrance it presumably blocks during some critical phase of adult life.

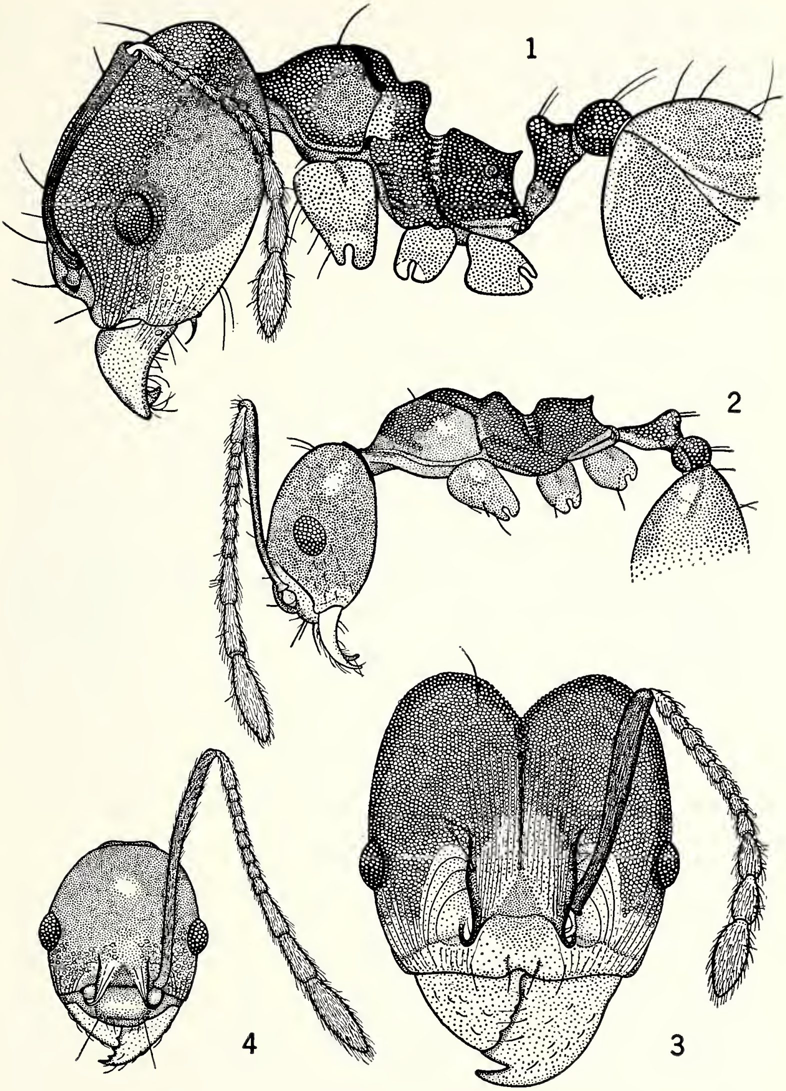
Pheidole embolopyx sp. nov. (Figs. 1-7)

Holotype soldier: TL (total outstretched length, including mandibles) 3.5, HL (length of head without mandibles) 1.03, HW (without eyes) 0.96, (Cephalic Index 93), WL (diagonal length of alitrunk in side view, without pronotal cervix) 0.91, scape L (chord to basal collar) 0.75, greatest diameter of compound eye 0.16 mm.

Form of head and body as in Figs. 1 and 3. Median sulcus of head reaching to frontal triangle; triangle and middle of clypeus smooth and shining, as are mandibles except for basolateral striation. As seen in perfect full-face view when held straight back, the scapes miss the apices of the occipital lobes by somewhat more than the width of the scape apex. The scapes appear more slender in some front views than they do in Fig. 3, and more curved towards the base (compare Fig. 1).

The alitrunk resembles those of *P. triconstricta* and *P. radoszkowskii,* with its deeply notched mesonotum and lesser constriction of the posterior pronotum along its suture with the mesonotum (indicated by black shading in Fig. 1). In dorsal view, raised but rounded humeri project from the middle of the pronotal sides. Propodeal dorsum sulcate its length, the sulcus wider behind.

Petiole slender, with a rather long anterior peduncle and anteroposteriorly compressed, almost squamiform node (W about 0.14 mm), with horizontal crest, vertical sides, and rounded corners as seen from behind. Postpetiole bun-shaped as seen from above, only about 1/3 wider than the petiole (W 0.20 mm) and its own length (0.14 mm); sides gently rounded in front, then nearly straight to posterior



Figures 1-4, *Pheidole embolopyx* sp. nov., side views of body and full-face views of head. Figures 1 and 3, holotype soldier; figures 2 and 4, worker minor from type nest series (M-77). Drawings by Margaret Menadue and the author, all to same scale.

border, which is very feebly constricted; no trace of lateral conules. Gaster (slightly dented) about 0.64 mm wide near the middle, with the usual subtruncate anterior end; strongly convex both above and below. Legs rather long and slender (longer than in *radoszkowskii*), but with moderately incrassate femora and tibiae.

Dorsum of head (face) densely reticulopunctulate and opaque, except for the shining areas noted above; area between frontal carinae and cheeks in front of eyes finely longitudinally costulate (Figs. 1 and 3). Sides of head behind (below) eyes, and all of ventral surface of head, smooth and shining. Alitrunk, both waist segments and basal 3/5 of first gastric tergite reticulopunctulate and opaque. Most of legs, a large spot on each side wall of pronotum, and most of gaster smooth and shining. Antennal scapes finely punctulate, weakly shining, with some indistinct longitudinal costulae mainly near base.

Longer erect setae, mostly bilaterally paired, arranged as shown in the figures (see especially Fig. 1). Head, mandibles, legs and gastric dorsum, especially the smooth surfaces, with sparse, fine, short appressed hairs. Scapes, femora, tibiae, coxae and trochanters each with 1-3 short, fine oblique standing hairs.

Color distinctive: body castaneous, including scapes, frontal triangle and posteromedian lobe of clypeus, margins of mandibles and frontal carinae, and the upper 3/4 of the sides of the head, including compound eyes (pattern shown in Figs. 1 and 3, especially the former); alitrunk and scapes darker than the rest, almost piceous. Legs and scapes dull brownish yellow. Dorsal surface and lower sides of head a contrasting light yellow, along with anterior clypeus and most of mandibles. This color pattern resembles at a glance that of *Pheidole punctatissima,* the common epiphyte dweller of Middle America.

Soldier variation: Of the paratypes, 4 soldiers were measured; a small specimen from sample M-77 has HL 1.00, HW 0.94 mm (CI 94), while the largest soldier in M-60 measures: TL 3.3, HL 0.08, HW 1.01 (CI 94), WL 0.91. The other soldiers are intermediate in size (HL), but one from the Igarapé Marianil berlesate has HL 1.07 by HW 1.02 mm (CI 95). Soldiers in the paratype series vary in depth of coloration, but the general pattern is the same. Some examples have an extra pair of erect hairs on the mesonotum.

Worker (from type nest series): TL 2.3, HL 0.58, HW 0.46 (CI 79), WL 0.75, scape L 0.73, greatest diam. eye 0.12 mm.

Form, sculpture and pilosity well portrayed in Figs. 2 and 4. Note the shape of the back of the head, rather narrowly rounded as seen

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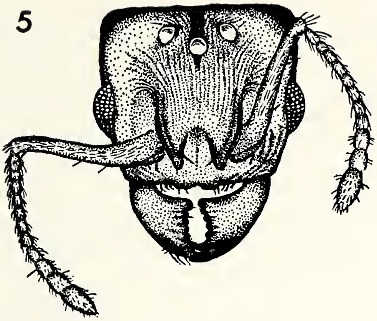

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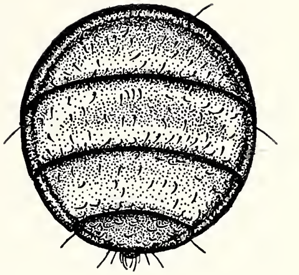

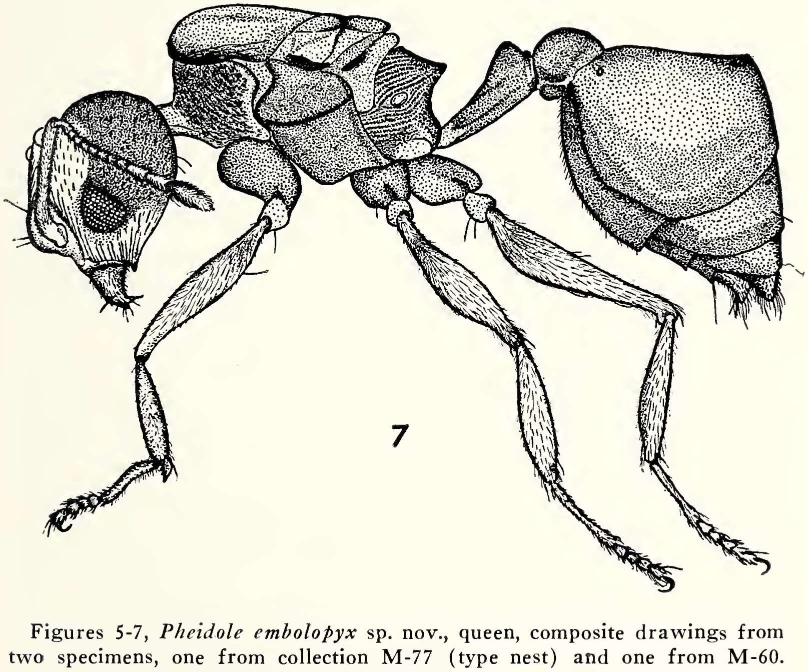

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Figures 5-7, *Pheidole embolopyx* sp. nov., queen, composite drawings from two specimens, one from collection M-77 (type nest) and one from M-60. Figure 5, head in full-face view. Figure 6, gaster viewed from behind to show face of "plug." Figure 7, side view of the whole insect. Drawings by Margaret Menadue, Frances McKittrick and the author, all drawn to the same scale, which is different from that of Figures 1-4.

in full-face view, with a narrow but distinct occipital collar. Except for the head, the sculpture is as in the soldier, but the reticulation of the postpetiolar disc and the anterior half of the gaster is more superficial, and the integument here somewhat shining. Head smooth, mostly shining, with sparse fine short appressed hairs in addition to the longer standing setae; anterior cheeks, especially the parts just mesad of the eyes, finely reticulopunctulate and subopaque, with fine costulae disposed as shown in Fig. 4. Mandibles smooth and shining, with sparse fine punctures. Outstanding pilosity positioned as in soldier.

Color light castaneous; mandibles, antennal funiculi and legs brownish yellow.

Worker variation: Of 6 paratype workers measured, only one differed from the specimen described above by much more than the average measurement error of about ± 0.01 mm; this is a worker from the Igarapé Marianil berlesate that is a little larger, darker and more heavily sculptured than others in the sample available: TL 2.4, HL 0.60, HW 0.49 (CI 81), WL 0.75 mm. It has the vertex largely microreticulate and subopaque instead of shining, and its color is prevailingly darker brown than the other workers. Otherwise, the workers show noticeable but not extreme variation in depth of coloration, and some have an extra pair of erect hairs on the mesonotum.

Female (dealate, from type nest series): TL 5.7, HL 1.00, HW 1.12 (CI 112), WL 1.65, scape L 0.80, greatest diam. compound eye 0.31, of median ocellus 0.11 mm.

Form shown in Figs. 5, 6 and 7. Head wide, with straight posterior margin in full-face view. Antennal scapes reaching posterior margin of head when held straight back, incrassate and strongly curved at base, the incrassate portion further thickened by a jacket of whitish gelatinous material that collapses in dried specimens (Fig. 5); this was much better developed in one specimen than in the other, and could possibly represent foreign material in part. Frontal lobes thick, a well-marked median sulcus extends from posterior border of head to a point in front of median ocellus. Clypeus with a feeble median carina in its posterior half.

Alitrunk robust, mesonotum broad and depressed, sides of scutum produced as thick curved shelves decidedly overhanging pronotum. Petiole with a broad (W 0.22 mm) transverse node, its rounded border emarginate in the middle as seen from behind; its peduncle strongly depressed and broadened (W 0.15 mm), with very convex margins as seen from above. Petiole subelliptical, about 0.56 mm wide, the sides produced as narrowly rounded angles, but not strictly speaking as conules.

Gaster of the highly modified form shown in Figs. 6 and 7. The truncate portion involves large parts of the first 4 tergites, which in the living, unswollen gaster fit together to produce a nearly flat circular disc surrounded by a heavy raised ridge that is continuous except for a small sector at the edge of the fourth segment. This disc is weakly shining, finely reticulate and with numerous very small, spaced tubercles with smooth, rounded heads; and also with small, curved, appressed pennant-shaped hairs.

Dorsum of head finely reticulopunctulate, with overlying costulation (striation) as shown in Figs. 5 and 7. Frontal area, middle of clypeus, upper surfaces of mandibles, "occipital" surface and a large area above and behind the compound eyes, extending to the ventral surface of the head, smooth and shining. The smooth areas of the back and sides of the cranium coincide almost exactly with the dark brown pigment pattern as shown in Figs. 5 and 7. Antennal scapes finely punctulate, shining, on apical halves. Alitrunk and legs predominantly smooth and shining, except for these striate to punctate-striolate areas: sides of pronoum (steeply oblique), anterior surface and lateral margins of scutum (horizontal, paralleling margins), sides of propodeum (prevailingly longitudinal, as shown in Fig. 7).

Petiole and postpetiole finely and densely punctulate, opaque, except for upper anterior surface of petiole, which is almost smooth and definitely shining. Base of gaster punctulate-striate, with radiating costulae, passing behind into a smooth, shining dorsal surface (in front of the truncate portion) and finely reticulate, shining sides; ventral base of gaster sculptured like the tergal base, but passing into shining, smooth and reticulate areas caudad.

Paratype female (dealate) from collection M-60, not measured, but nearly the same size as the queen of the type nest, described above. The scape bases of the paratype are thicker, and originally carried more of the whitish gelatinous substance.

Holotype soldier (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA) taken together with queen, other soldiers, workers and brood, from a small colony (M-77) nesting in rotten wood on the rain forest floor near the Igarapé Marianil, which is a small creek just beyond Kilometer 5 on the Rio Branco Road after its branching from Amazonas Ruta 1 ("Itacoatiara Highway"). The road fork is 19 km NE of Manaus, and the igarapé is about 24 km NE of Manaus by road. This forest is on undulating country with sandy soil. Although the forest was very dark and did not appear to be seriously disturbed, we found few really large trees, and there were many spiny palms in the undergrowth. Probably the area had been selectively logged (26 August, 1962, W. L. Brown, Jr. leg.).

Workers and soldiers (labeled "BF") were also taken in leaf-litter berlesates from the vicinity of Igarapé Marianil during the same month, and the other paratypes (M-60) came from partially newly cut hillside rain forest near kilometer 50 on the western side of Amazonas Ruta 1 (24 August 1962, Brown leg.). The M-60 ants were nesting in a small spongy piece of rotten branch (without bark) on the forest floor. The soil was sandy, with thin litter, and the country looked very much like that at Igarapé Marianil, about 30 km to the west. The phragmotic nature of neither queen was noticed until after they had been captured, and so no particular note was made of their behavior or position within the nests.

Paratypes are deposited with the holotype and in the collections of W. W. Kempf and Cornell University, Ithaca, New York.

Pheidole embolopyx appears to belong to the *triconstricta* group, but the color and sculpture of the soldier, as well as the narrowly-rounded occiput of the worker minor, will separate the new species from the several forms clustered around *P. triconstricta* and *P. radoszkowskii.* The types have been compared with all likely related species in the Museum of Comparative Zoology, the W. W. Kempf (ex-Borgmeier) Collection, and several of the principal European ant collections, and are thought to be distinct. The queen is of course unique in form among *Pheidole* known from this caste, but for most New World members of the genus, the queen remains undescribed. After all is said and done, *P. embolopyx* may eventually end in the synonymy of some named species I have not taken into account. Certainly, the known described and undescribed New-World species of *Pheidole* number in the hundreds, and they remain unrevised. The biological interest of this particular species dictated that it should be described without further delay, regardless of the small risk that it might turn out to have received a name previously.

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THE SPIDER GENUS *BILLIMA* SIMON*

By Herbert W. Levi

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Simon (1908) described the species *Billima attrita* which he placed in the subfamily Theridiosomatinae. Recently I noticed that Bonnet (1959, p. 5042) placed the genus in the subfamily Argiopinae. As I just revised the American species of the subfamily, an examination of the type specimen appeared in order.

I would like to thank Prof. M. Vachon and M. Hubert for the loan of the specimen from the Muséum National d'Histoire Naturelle, Paris.

Billima attrita is a theridiid. It does not belong in the family Araneidae (= Argiopidae) or to the Theridiosomatidae as it lacks a colulus, has only one tooth on the chelicerae, and the labium is not rebordered. All members of both the Araneidae and Theridiosomatidae have a large colulus, and usually have numerous teeth on the chelicerae and a rebordered labium. *Billima attrita* belongs to the genus *Theridion* (Levi and Levi, 1962). A description is presented here and the species is illustrated for the first time.

Theridion Walckenaer

Theridion Walckenaer, 1805. Type species designated by Int. Comm. Zool. Nomencl. Opinion 517, 1958: *Aranea picta* Walckenaer 1802. *Theridion* is listed in the Official List of Generic Names in Zoology.

Billima Simon, 1908. Type species by monotypy *B. attrita*. NEW SYNONYMY.

Theridion attrita (Simon)

Figs. 1-4

Billima attrita Simon, 1908, p. 430. Female lectotype here designated and juv. male paralectotype from "Stat. 109 Subiaco N." [Perth, West. Australia] in the Muséum National d'Histoire Naturelle, Paris, examined. — Bonnet, 1955, p. 887. Not *Theridion attritum* Nicolet 1849 (=*Anelosimus attritus*).

Description. Carapace yellowish with black line all around. Sternum yellow-orange with gray pigment. Legs yellow with darker marks on venter. Dorsum of abdomen whitish with a median darker longitudinal band, irregular in outline and bordered on each side by a white band (Fig. 1); venter black with a white transverse pigment band (Fig. 2). Eyes subequal in size. Anterior median eyes slightly more than one diameter apart, their radius from laterals.

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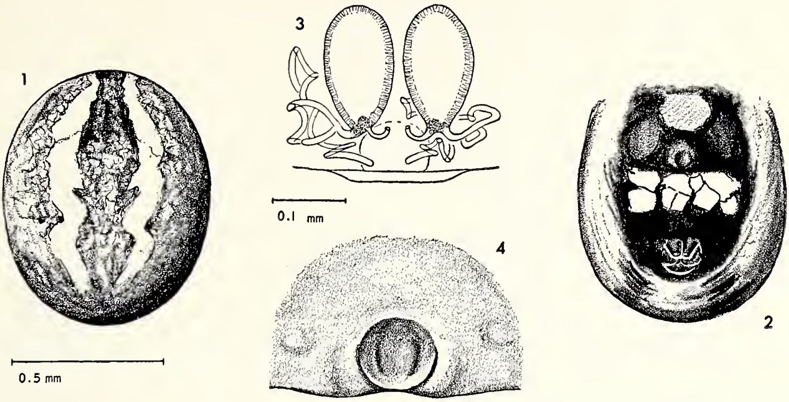

Figs. 1-4. *Theridion attritum* (Simon), female. 1. Dorsum of abdomen. 2. Venter of abdomen. 3. Female genitalia, dorsal view. 4. Epigynum.

Posterior eyes their diameter apart. Labium attached to sternum with indistinct seam. One tooth on anterior border of chelicerae. Legs quite short, abdomen suboval (Fig. 1). Epigynum has a central circular depression containing the openings (Fig. 4). Connecting ducts of epigynum coiled (Fig. 3). Total length, 2.2 mm. Carapace 0.7 mm long, 0.7 mm wide. First femur, 0.8 mm, patella-tibia 1.0 mm, metatarsus 0.7 mm, tarsus 0.4 mm. Second patella and tibia 0.8 mm, third 0.5 mm, fourth 0.8 mm.

This species is surprisingly similar to *Theridion melanurum* Hahn of Europe and *Theridion varians* Hahn. However, it is much smaller and the internal ducts differ in structure (Fig. 3). The ventral transverse band on the abdomen (Fig. 2) would be unusual in American and European *Theridion* species.

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STUDIES ON THE SYSTEMATICS OF THE BEROTHIDAE, PART I: A REDESCRIPTION OF THE GENUS *SPHAEROBEROTHA* NÁVAS, WITH A CRITIQUE OF THE TAXONOMIC CHARACTERS USED IN THE BEROTHINAE (NEUROPTERA)

By Ellis G. MacLeod[1]

INTRODUCTION

As a by-product of the recent review by P. A. Adams and myself (MacLeod and Adams, 1967) of the subfamily classification of the Berothidae, new information has been uncovered concerning the identity and taxonomic status of some of the more poorly known members of this family. Because of the general difficulty in securing type specimens for study and because of the great paucity of these insects in most collections, I do not consider it advisable to undertake, at this time, the full, species-level revision which this family so badly needs. Nevertheless, sufficient data are now at hand to encourage the view that a long-term, piecemeal study of the more disorderly sections of the family may ultimately produce a better taxonomic understanding of these insects.

Accordingly, the present series of publications has been initiated for the purpose of providing a vehicle for the redescription of key genera and species, for the discussion of the taxonomic utility of various systematic characters, for the reevaluation of the validity and systematic position of the numerous genera of the Berothinae, and for the publication of such ecological and morphological information as provides insight into the adaptive basis of certain evolutionary specializations. If successful, this approach should eventually produce at least a partial, generic-level revision of the family and should lay a better foundation for a future, thoroughgoing revision of the species than exists at the present time.

The first paper of this series will be devoted to a redescription of the poorly known genus *Sphaeroberotha* Navás and to a preliminary discussion of the relationships of certain genera of the Berothinae. In the course of this discussion I have set forth my views concerning the usefulness of certain of the generic-level taxonomic characters

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which have been used in the past and have noted which additional characters I feel should be carefully evaluated in future descriptive and taxonomic work with this family.

The Genus *Sphaeroberotha*

Navás based his description of the type species of *Sphaeroberotha, S. dumonti,* on a single female. Although he included the species *Costachella geyri* (Esben-Petersen) in his new genus as a second species, his characterization of *Sphaeroberotha* was, in fact, based almost solely on *S. dumonti* since he had only a drawing, whose accuracy he questioned, of the wings of Esben-Petersen's species for study. Through the great kindness of Dr. S. Kelner-Pillault of the Muséum National d'Histoire Naturelle, Paris, I have been permitted to borrow and study the holotype of *S. dumonti* from which the following redescriptions and discussions are drawn.

Sphaeroberotha Navás

Sphaeroberotha Navás, 1930, Broteria 26: 133-134. Type species (by original designation): *Sphaeroberotha dumonti* Navás, 1930. Tjeder, 1958, South African Animal Life 6: 281-282. MacLeod and Adams, 1967, Psyche 74: 254, 256, 258.

Description. A genus belonging to the Berothinae. Face short, extending only slightly ventrad of eyes; vertex a slightly raised triangular area, with two weak lateral tubercles at its posterolateral corners; postgenae moderately inflated. Scape only slightly elongate; antennomeres distal to scape subspherical, each with two rings of distally directed setae which extend as far as the next antennomere; distal antennomere more elongate, acuminate. Mouthparts well developed, mandibles with tips crossing when jaws are closed. Pronotum moderately robust, slightly wider than long, with two transverse furrows, strongly deflexed laterally. Fore legs lacking raptorial modifications.

Wings (Fig. 1) elongate, with rounded tips, lacking any indication of falcation; Sc connected distally to R_1 by an oblique cross vein at edge of pterostigma; two radial cross veins; free basal piece of MA (Fig. 1, b) oblique, slightly proximal to basal fork of MP; a weak series of outer gradate crossveins present. Fore wing: probable vestige of recurrent humeral vein present basally in costal cell as a steeply inclined crossvein with a distal fork; stems of M and R fusing just proximal to basal subcostal crossvein; outer gradate crossvein between the branches of MP generally in line with gradates above and below this vein, not far proximal to these; jugal vein and lobe absent; with weakly developed lines of flexion present between MA and MP and between CuP and 1A; crossveins and forkings lacking dense tufts of erect setae; similar dense tufts from trichosors of wing margin also lacking. Hind wing: with C and Sc running very closely together for most of distance from wing base to pterostigma; no basal crossvein in subcostal space; stem of M passing beneath R, but free from this vein to base of wing; CuA paralleling posterior margin and reaching into distal 1/3 of wing, with numerous pectinate marginal forks; no trace of CuP present; jugal vein absent; a weak line of flexion developed between bases of M and R, continuing a short distance distal to the basal free piece of MA.

Male unknown. Female (Figs. 2, 3, 4): 7th sternite (Figs. 2, 3, 7S) widely unsclerotized posteriorly and in midline, represented as two separated bilateral pieces, without the development of thin, rod-like lateral sclerites; 8th sternite (Figs. 2, 3, 8S) thin and strap-like laterally, with an anteriorly directed median lobe; 8th gonocoxites (Figs. 2, 3, 8gcx) represented as a small concave sclerite just anterior to gonopore; 9th gonocoxites (Figs. 2, 3, 9gcx) large, with well-developed, elongate hypocaudae; 9th gonapophyses lacking; 10th sternite (Fig. 3, 10S) represented as a weakly sclerotized area dorsad of 9th gonocoxites; genital chamber (Fig. 2. gen. ch.) large, with duct from collaterial gland emptying into it posteriorly, widely confluent with copulatory bursa (Figs. 2, 3, 4, cop. b.), closed by anteriad appression of membranous area between 9th gonocoxites against large convex lobe of weakly sclerotized cuticle just posteriad of 8th sternite; copulatory bursa somewhat small, consisting of membranous distal portion and a well-sclerotized, coiled proximal area from which the spermathecal duct originates; spermathecal duct (Fig. 4, sp. d.) elongate and looped; spermatheca (Figs. 2, 4, sp.) intricately coiled, sclerotized, with a prominent spherical diverticulum and with apparent cuticular attachments for glandular epithelium along one side just proximal to origin of fertilization canal; fertilization canal lacking usual fringe of cuticular attachments for glandular epithelium (Fig. 4, fert. c.).

Type species: *Sphaeroberotha dumonti* Navás.

Sphaeroberotha dumonti Navás

Sphaeroberotha dumonti Navás, 1930. Broteria 26: 134-135, fig. 44. Described from a single female now located in the collections of the Muséum National d'Histoire Naturelle, Paris, MacLeod and Adams, 1967, Psyche 74: 254.

Description. Face and vertex dark yellow, with stout white setae of moderate length and with a suggestion of dark spotting about the bases of the vertex setae; labrum with a transverse row of thinner, more-elongate setae. Scape short, twice as long as broad, setae like those of vertex but darker, right antenna with fifty-six antennomeres distal to scape, each with a thin brown ring, setae of a dark amber color. Thorax tannish brown (probably much discolored), with no indications of any original mottling of color pattern. Prothoracic legs pale yellow, femora and tibiae with a few scattered darker spots.

Wings (Fig. 1) with anterior margin of fore wing slightly concave; no maculations on membrane, but with longitudinal veins of fore wing with dark dots at setal bases; outer gradate series with 4 crossveins in the anterior wing, 3 crossveins in the posterior wing; fore wing length 6.7 mm.

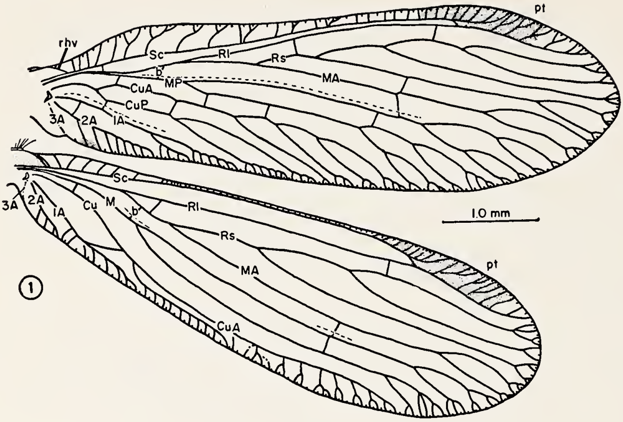
Thorax and wing margin with sparse elongate white setae (probably mostly rubbed off), posterior wing margins with more-elongate, silky pale yellow setae; setae on wing veins white, shorter than those on body, directed basally at about a 45° angle to longitudinal axis of vein, length about equal to average distance between veins; no evidence of squamae on body, legs, or wings.

Abdominal structures as in Figs. 2-4: 8th sternite with short setae and with an apodeme reenforcing the strap-like lateral arms, anteriorly directed median lobe slightly pedunculate in lateral view, somewhat spatulate in shape when viewed ventrally; cuticle between 8th sternite and 8th gonocoxites a weakly sclerotized convex lobe; 9th gonocoxites somewhat triangular in lateral aspect, with a distinct posterior lobe. Sclerotized, proximal portion of bursa wound in a snail-like coil of decreasing diameter, from the tip of which the spermathecal duct originates; spermatheca with coiling pattern as in Fig. 4.

The pinned type is missing its left antenna distal to the scape, right fore leg distal to the femur, mesothoracic legs distal to their coxae, metathoracic legs distal to the coxa (right) and femur (left) and most of the left hind wing. The abdomen has been removed, cleared, and placed in glycerine in a microvial on the pin with the specimen. The holotype was collected at a light in May, 1927 by C. Dumont at Nefta, Tunisia.

Discussion

Such specialized features as the large, anteriorly directed 8th sternum, well-developed hypocaudae, manner of closure of the genital



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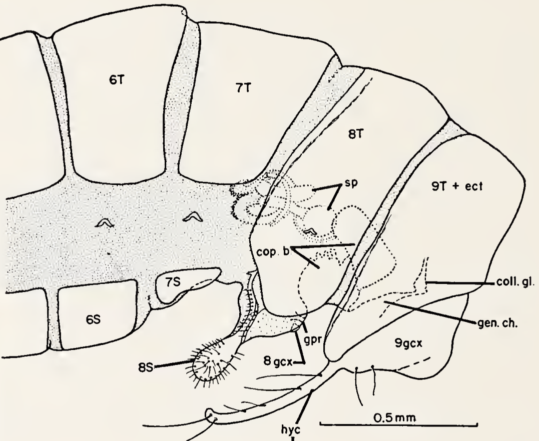

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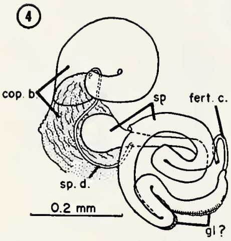

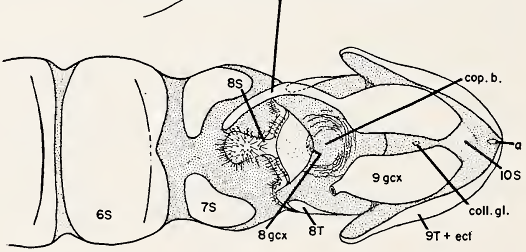

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MACLEOD — BEROTHIDS

chamber, and elongate wings show that *Sphaeroberotha* quite properly belongs to the Berothinae. Within this group, however, its systematic position is far from clear. Indeed, because of the poor state of our knowledge concerning many other genera of the Berothinae, it is not even certain that *Sphaeroberotha* represents a valid genus.

Along with the berothines *Protobiella* Tillyard, *Spermophorella* Tillyard, *Nodalla* Navás, *Costachillea* Navás, and *Cycloberotha* Navás, *Sphaeroberotha* shares the feature of a rounded outer wing margin. However, as the members of the other three subfamilies of the Berothidae share this same characteristic, by itself such a similarity shows nothing about the relationships of these genera of the Berothinae. These six genera do, however, possess certain other similarities and, as they have, to varying degrees, been treated as a unit in previous taxonomic works, they will be considered together here.

Prior to his description of *Sphaeroberotha,* Navás himself (1929) separated the first three of these genera[2] from the other two by the presence of a fusion between Sc and R_1 in the region of the pterostigma which was presumed to be lacking in *Costachillea* and *Cycloberotha* (and in the subsequently described *Sphaeroberotha*) where

EXPLANATION OF PLATE 37

Drawn from the female holotype of *Sphaeroberotha dumonti* Navás in the Muséum National d'Histoire Naturelle, Paris. All from camera lucida tracings. Fig. 1. Right fore- and hindwing. Figs. 2 and 3. Lateral and ventral aspects of the tip of the abdomen. (Setae indicated only on 8th-sternite, 9th gonocoxites, and hypocaudae. Right hypocauda omitted from Fig. 3.) Fig. 4. Copulatory bursa and spermatheca, dorsal aspect with posterior end directed toward top of page.

Abbreviations: a — anus; 1A, 2A, 3A — 1st, 2nd, 3rd anal veins; b — basal free piece of anterior median vein; coll. gl. — collaterial gland duct and opening; cop. b. — copulatory bursa; Cu — base of cubital vein; CuA — anterior cubitus; CuP — posterior cubitus; fert. c. — fertilization canal; 8 gcx, 9 gcx — 8th, 9th gonocoxites; gen. ch. — genital chamber; gl? — possible cuticular canals from spermathecal gland cells; gpr — gonopore; hyc — hypocauda; M — base of median vein; MA — anterior median vein; MP — posterior median vein; pt — pterostigma; R1 — first branch of radial vein; Rs — radial sector; rhv — vestige of recurrent humeral vein; 6S, 7S, 8S, 10S — 6th, 7th, 8th, 10th sternites; Sc — subcostal vein; sp — spermatheca; sp.d. — spermathecal duct; 6T, 7T, 8T — 6th, 7th, 8th tergites; 9T + ect — fused 9th tergite and ectoproct.

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[2] Navás further separated these three genera by placing *Protobiella* and *Spermophorella* in one tribe, the Spermophorellini, and *Nodalla* in a second tribe, the Nodallini. No diagnostic features by which these two tribes might differ are apparent from his descriptions; indeed the Spermophorellini are not even included in his key to tribes (pp. 17-18) in his revision of 1929!

these veins are united by a short crossvein. This opposing set of characters has been much used in the supraspecific taxonomy of the Berothidae, although there are several complicating features of this area of the wing which undermine the usefulness of this set as a taxonomic character.

For example, there are many cases in which the approach of Sc and R_1 is so close that the decision as to whether these veins are actually fused or not becomes arbitrary. A more subtle source of confusion arises from variations in the degree of obliquity of the crossvein, so that in some cases an apparent fusion of Sc and R_1 occurs when in reality these veins are quite separate. The ease with which this condition can mimic a fusion of these veins is further compounded by the fact that the true termination of Sc is often masked in the thickening and pigmentation of the adjacent pterostigma. In addition to these complexities, this set of taxonomic characters is also often subjected to a high degree of individual variability. I feel, therefore, that the degree of fusion of these veins is of a limited utility and that the use of this feature at the tribal level can probably not be justified. On this basis, then, the genera *Protobiella, Spermophorella,* and *Nodalla* cannot be excluded from consideration in ascertaining the relationships of *Sphaeroberotha.*

Costachillea has been considered to differ from *Sphaeroberotha* and *Cycloberotha* by the presence of an "internal radial vein" (*i.e.* the vein labeled b in Fig. 1 of the present paper) in these latter two genera, which is presumed to be lacking in *Costachillea.*[3] Here again

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[3] Because of the rather far distal position of the basal piece of MA in many berothids, it might be considered that this vein is a true crossvein, the real basal piece having been lost with the close approximation of the stems of R and M. This possibility seems to be strengthened by the fact that in the fore wings of several genera (*Trichoberotha* and some species of *Lomamyia* show this especially well) there does seem to be an additional, more proximal vein between the nearly adjacnt bases of R and M at the level of the m-cu crossvein, which is the more usual location of the basal piece of MA in most other Neuroptera.

I feel, however, that this more proximal crossvein is a secondary development in those genera where it is present and that the true basal piece of MA is really the more distal vein. My principal reason for this conclusion is that I am unable to find a second, more-proximal vein in the fore wings of such generalized berothids as *Cyrenoberotha* and *Rhachiberotha,* where the bases of R and M are rather widely separated and where such a vein, if present, should be easily seen. Again, in the even more generalized berothid relatives of the Neurorthidae and Dilaridae, where the relationships of the veins at the base of the fore wing are equally well made out, only a single vein is present between these longitudinal veins, which in the nallachiine one can, I feel, maintain strong reservations about the importance of this set of alternatives as a taxonomic character. The degree of development of the basal piece of MA is subject to a good deal of variation, largely because of the weakening of its sclerotization which results from the line of flexion passing through it. This difficulty in detecting the vein is compounded when the vein is located in a relatively more proximal position between the approaching bases of R and M.[4] As a result of these considerations, I believe that it would be premature to assume that *Costachillea* cannot be closely related (or perhaps congeneric) with *Sphaeroberotha* until, at a minimum, specimens of *Costachillea* have been examined to see if perhaps a poorly sclerotized basal piece of MA is not present after all which was missed by Navás.

The final genus of berothines with rounded wing apices which should be considered is *Cycloberotha.* The characters which have seemed to separate this genus from *Sphaeroberotha* are the number of radial crossveins, the number of branches of the radial sector, and the presence or absence of squamae on the females. With respect to the number of radial crossveins, Navás (1929, 1930) has stated that *Cycloberotha* is characterized by the possession of three. Although this is true for the type species, *C. mjobergi* (Esben-Petersen), Navás has erred in evaluating this feature in the second species of this genus, *C. neuropunctata* (Esben-Petersen), where only two radial crossveins are present. Esben-Petersen (1917) states this quite clearly in his original description of this species and I have verified this fact from the examination of a series of specimens of this species in my collection. The number of radial crossveins is frequently rather constant within groups of closely allied species and it may be that *C. neuropunctata* has been incorrectly assigned to *Cycloberotha.* Precedent, however, exists in both *Berotha* and in the rather well-studied *Lomamyia* for including in the same genus species with differing numbers of radial crossveins so that *C. neuropunctata* should not be excluded from *Cycloberotha* on the basis of this feature alone. In any

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Dilaridae is relatively distal in position and is slightly sinuate as it is in the fore wings of many berothids. Unfortunately, comparisons with the closest relatives of the Berothidae, the Mantispidae, cannot be drawn, since even in the most generalized of the Platymantispinae, the bases of R and M of the fore wing are too closely adjacent to permit study.

[4] In evaluating Navás' descriptions an additional, essentially semantic problem is added to these sources of confusion: a vein is only an "internal radial vein" if it is located proximal to the fork of MP. Where the vein is located distal to this fork it no longer qualifies as an "internal radial vein" and the taxon is described as lacking the vein (cf. Navás, 1929, p. 23).

case, attempts to separate *Sphaeroberotha* and *Cycloberotha* on the strength of this single character is made impossible by the present heterogeneous composition of *Cycloberotha.*

The number of branches of the radial sector is likewise unsuitable as a criterion for distinguishing these two genera, since *C. neuropunctata* and *S. dumonti* both have an identical pattern of branching of the radial sector. It is true that the type specimen of *C. mjobergi* has one fewer branch in the radial sector of the fore wing, but as has been recently noted (MacLeod and Adams, 1967) slight differences in the number of branches of the radial sector are probably too variable a feature to use as a taxonomic character of generic distinction. The presence of squamae on the females of *Cycloberotha* is likewise an insufficient reason for separating these two genera, since otherwise closely related species are known in both *Berotha* and *Lomamyia* which differ in the presence or absence of these squamae on their females.

With the present state of our knowledge concerning the genera presumed to be somewhat related to *Sphaeroberotha,* it is not possible to more than guess at what the diagnostic features of the genus might be, assuming that it is actually a valid entity. Certainly none of the taxonomic characters discussed above is sufficiently free from suspicion to serve as a guide in this direction. As a tentative guess, since I have not observed them in the form seen in *Sphaeroberotha* elsewhere in the family, I might suggest that the sclerotized, "snail-shell" specialization of the proximal portion of the copulatory bursa and the presumptive glandular elements associated with the distal portion of the spermatheca (rather than in their more usual position along the fertilization canal) may perhaps prove of diagnostic importance. There is a similar sclerotization of this portion of the copulatory bursa in *Cyrenoberotha* of the distantly related Cyrenoberothinae, although here the sclerotized portion is not coiled and of course there are many other differences. Again, in the somewhat more closely related *Naizema* (but not in *Trichoberotha*), there is a tendency for a weak sclerotization of this portion of the copulatory bursa (MacLeod and Adams, 1967). Here again, however, there is no tendency for a coiling of this sclerotized portion. Finally, *Trichoberotha* (to be redescribed in a subsequent paper of this series) has a superficially similar, snail-like coil in the sperm-conducting pathway; however, here it is the spermatheca itself, rather than a portion of the copulatory bursa, which shows the apparent similarity. There are, in addition, many other important differences between *Sphaeroberotha* and *Trichoberotha.*

The foregoing analysis, which I regret has been unable to settle any question as to the position or validity of *Sphaeroberotha,* emphasizes the great need for a better understanding of the detailed structure of a large segment of the species and genera of the Berothinae.[5] Future descriptive work must carefully re-evaluate the effectiveness of the taxonomic characters which have been used in the past and must make available the condition of characters whose importance has usually not been properly appreciated up until now. In particular, I feel that among the more important features for the characterization of valid genera are the structure of the male and female genitalia and of the internal, sperm-conducting and storage system of the female. Such details of the male as the degree of development of the gonarcus and gonocoxites and the basic form and length of the mediuncus and its terminal setae will probably be of great help in this attempt. In the female, the size and shape of the 7th and 8th sternites, the degree of development of hypocaudae, the presence or absence of 9th gonapophyses, and, especially, the structural details of the copulatory bursa and spermatheca should also be carefully evaluated.

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[5] Through the courtesy of Dr. O. S. Flint, the berothids of the Neuroptera collection of A. Alfieri, recently acquired by the U. S. National Museum, have been loaned to me for study. The collection contains specimens of *Nodalla,* including the holotype of *N. aegyptiaca* Navás, the type species of this genus. Preliminary study of these specimens reveals the same basic pattern of wing venation and female genitalia as *Sphaeroberotha* and indicates a probable synonymy of these two taxa. This material will be described in a future paper of this series.

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A regular meeting of the Club is held on the second Tuesday of each month October through May at 7:30 p.m. in Room B-455, Biological Laboratories, Divinity Ave., Cambridge. Entomologists visiting the vicinity are cordially invited to attend.

The illustration on the front cover of this issue of Psyche is a reproduction of the drawing of the first Cretaceous ant, *Sphecomyrma freyi* Wilson and Brown, from amber collected near Newark, New Jersey (Psyche, vol. 74, p. 1, 1967).

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